

**Colorado River Cutthroat Trout
(*Oncorhynchus clarkii pleuriticus*):
A Technical Conservation Assessment**



**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

October 10, 2008

Michael K. Young, Ph.D
USDA Forest Service, Rocky Mountain Research Station
800 East Beckwith Avenue
Missoula, Montana 59801

Peer Review Administered by
[American Fisheries Society](#)

Young, M.K. (2008, October 10). Colorado River Cutthroat Trout (*Oncorhynchus clarkii pleuriticus*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: <http://www.fs.fed.us/r2/projects/scp/assessments/coloradorivercutthroattrout.pdf> [date of access].

ACKNOWLEDGMENTS

I thank Todd Allison, Warren Colyer, Greg Eaglin, Noah Greenwald, Paula Guenther-Gloss, Christine Hirsch, Jessica Metcalf, Dirk Miller, Kevin Rogers, and Dennis Shiozawa for their comments on an earlier version of this manuscript. My thanks also to Claire McGrath, Bruce Rosenlund, and Dave Winters for their reviews of a similar manuscript on a related subspecies. I appreciate the assistance of Dennis Shiozawa, Brigham Young University; Bill Wengert, Wyoming Game and Fish Department; and Dan Brauch, Colorado Division of Wildlife, for sharing a number of unpublished reports. This work was funded by the Species Conservation Project for Region 2 and the Rocky Mountain Research Station, both part of the USDA Forest Service.

AUTHOR'S BIOGRAPHY

Michael Young has been a Research Fisheries Biologist with the USDA Forest Service Rocky Mountain Research Station since 1989. His work focuses on the ecology and conservation of native coldwater fishes and the effects of natural and anthropogenic disturbances on stream ecosystems.

COVER ILLUSTRATION CREDIT

Illustration of the Colorado River Cutthroat Trout (*Oncorhynchus clarkii pleuriticus*) by © Joseph Tomelleri.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE COLORADO RIVER CUTTHROAT TROUT

Status

The Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) was once distributed throughout the colder waters of the Colorado River basin above the Grand Canyon, primarily in Colorado, Utah, and Wyoming. Primarily a fluvial species, it is believed to have historically occupied about 34,500 km of streams, of which about 4,850 km are currently occupied by fish thought to be good representatives of this taxon and about 2,900 km are occupied by unhybridized populations or those of particular ecological significance. Somewhat less than half of these populations are found in USDA Forest Service (USFS) Region 2, but all the national forests where Colorado River cutthroat trout historically occurred—Arapaho-Roosevelt, Grand Mesa-Uncompahgre-Gunnison, Medicine Bow-Routt, San Juan, and White River—still support populations. The increased awareness of the status of this subspecies and increased agency conservation efforts since the 1970's have apparently arrested the rapid loss of known populations and established new populations in some areas.

The Colorado River cutthroat trout was first petitioned for listing as threatened or endangered under the Endangered Species Act in December 1999, but in April 2004, the U.S. Fish and Wildlife Service (USFWS) concluded that this subspecies did not warrant listing. In June 2007, the USFWS issued a 12-month finding that this subspecies still did not warrant listing under the Endangered Species Act. Regions 2 and 4 of the USFS have designated the Colorado River cutthroat trout a sensitive species; the Bureau of Land Management has accorded it a similar status; and Colorado, Utah, and Wyoming have given it special management designations. A multi-agency agreement also provides oversight for management of this subspecies.

Primary Threats

Historically, habitat alteration from mining, agriculture, and water development contributed to the extirpation or reduction of large numbers of populations of Colorado River cutthroat trout, whereas introductions and invasions of nonnative trout probably represent the greatest cause of recent declines and the major impediment to restoration of this fish in much of its historical range. Many populations appear to remain vulnerable to this threat either because barriers to ongoing invasions are absent or because existing barriers may be temporary or have nonnative fish passed over them illegally. A lack of connectivity to other populations increases their vulnerability to extirpation from “short term” natural disturbances such as fire, post-fire debris torrents, or floods. In the long term the loss of genetic variability and the potential for evolving in response to changing environmental conditions can occur with limited population size. Some climate change model projections suggest suitable habitats may shift to higher elevations and precipitation patterns imply there may be large declines in late summer flows. The lack of connectivity could exasperate this problem by not allowing mobility to suitable habitats. While state and federal agencies along with public organizations are working to reestablish Colorado River cutthroat trout populations, the cumulative effects of past and ongoing impacts coupled with greater resource demands (particularly for water) by a rapidly growing human population in the Rocky Mountains, makes the future for Colorado River cutthroat trout uncertain.

Primary Conservation Elements, Management Implications, and Other Considerations

Conservation of Colorado River cutthroat trout will require attention to both short-term and long-term threats. In the short term, preventing invasions by nonnative trout through the judicious use of barriers can protect some populations, but perhaps the most successful long-term strategy will be to eliminate nonnative trout from downstream waters and expand the distribution of Colorado River cutthroat trout into larger basins exhibiting greater connectivity. Removal of nonnative trout and reintroduction of Colorado River cutthroat trout into formerly occupied habitats will also reduce the probability of losing all local populations simultaneously as well as offer the potential to conserve the remaining genetic variability represented in extant populations. Habitat improvement may have beneficial effects, particularly if combined with whole-basin changes in activities that degrade habitats; however, acknowledging the inherent temporal variability in habitat quality is essential. Given that habitat change is inevitable,

managing to permit the continued evolution of this subspecies may be fundamental to its long-term persistence. A strategic, rather than opportunistic, approach to conservation of Colorado River cutthroat trout is likely to be the most efficient and successful.

TABLE OF CONTENTS

ACKNOWLEDGMENTS	2
AUTHOR'S BIOGRAPHY	2
COVER ILLUSTRATION CREDIT	2
SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE COLORADO RIVER CUTTHROAT TROUT	3
Status	3
Primary Threats	3
Primary Conservation Elements, Management Implications, and Other Considerations	3
LIST OF TABLES AND FIGURES	7
INTRODUCTION	8
Goal	8
Scope	8
Treatment of Uncertainty	8
Application and Interpretation Limits	9
Publication on the World Wide Web	10
Peer Review	10
MANAGEMENT STATUS AND NATURAL HISTORY	10
Management Status	10
Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies	11
Biology and Ecology	12
Systematics and general species description	12
Distribution and abundance	13
Population trend	15
Activity pattern and movements	16
Territoriality	16
Diel movements	16
Seasonal movements	17
Life-history-related movements	17
Habitat	18
Temperature	19
Channel units and structure	19
Cover and complexity	20
Spatial patterns and temporal dynamics	21
Diet	22
Spawning	22
Demography	23
Life history characteristics	23
Population structure: survival rates and temporal patterns	25
Population models	25
Genetic structure	27
Metapopulations	27
Community ecology	28
Sympatric vertebrates	28
Parasites and diseases	28
Envirogram	28
CONSERVATION	34
Potential Threats	34
Nonnative fishes	34
Brook trout	34
Brown trout	35
Rainbow trout and nonindigenous cutthroat trout	36
Other nonnative species	37

Genetic concerns	38
Inbreeding depression and loss of genetic variation.....	38
Unintentional selection.....	38
Harvest and recreation.....	40
Abiotic events and processes.....	40
Habitat fragmentation.....	40
Anthropogenic habitat degradation	41
Natural disturbance.....	43
Climate change	45
Conservation Status in Region 2.....	46
Potential Management in Region 2.....	46
Implications and potential conservation elements	46
Tools and practices	48
Population and habitat monitoring	48
Population and habitat management approaches.....	54
Information Needs.....	61
DEFINITIONS.....	64
REFERENCES	66

EDITOR: David Winters, USDA Forest Service, Rocky Mountain Region

LIST OF TABLES AND FIGURES

Tables:

Table 1. Parameter values for the components of the matrix population model and ranges of values for those parameters	26
---	----

Figures:

Figure 1. The number of peer-reviewed journal articles on subspecies of inland cutthroat trout and nonnative trout.	9
Figure 2. The current and historical ranges of Colorado River cutthroat trout, based on expert opinion.	14
Figure 3. Envirogram of factors important to the different life stages of Colorado River cutthroat trout.....	29

INTRODUCTION

This assessment of the Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) is one of many being produced to support the Species Conservation Project for the USDA Forest Service (USFS) Rocky Mountain Region (Region 2). The Colorado River cutthroat trout is considered a sensitive species in Region 2. Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of a significant current or predicted downward trend in abundance or habitat quality that would reduce its distribution (FSM 2670.5 (19)). Because of concerns about its viability and abundance, a sensitive species requires special management, so knowledge of its biology and ecology is critical.

Goal

The purpose of this species conservation assessment is to provide forest managers, scientists, and the public with a thorough discussion of the current understanding of the biology, ecology, conservation status, and management of Colorado River cutthroat trout. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to develop specific management recommendations. Rather, it provides the ecological background upon which management can be based and focuses on the consequences of changes in the environment from natural and anthropogenic sources that are relevant to the management of Colorado River cutthroat trout. Furthermore, it considers the implementation and success of management recommendations for the conservation of this species. Admittedly, any assessment of the biology, threats, and possible management of a species reflects the expertise and biases of the author. Herein I emphasize science and management directed toward the understanding, conservation, and restoration of indigenous populations and their phenotypic and genotypic diversity, and devote little attention to populations established or maintained primarily for recreation. Although there is much we do not know about ecosystem processes, I stress a conservative and precautionary approach that favors restoring those processes as opposed to more direct intervention that often has unintended consequences; in other words, adopting the physician's (and ecologist's; Leopold 1949) creed of do no harm. Other perspectives would highlight different ecological aspects, threats to persistence, and management opportunities.

Scope

This assessment focuses on Colorado River cutthroat trout within the USFS Rocky Mountain Region. Although the vast majority of literature on cutthroat trout and nonanadromous salmonids in montane habitats originates from research elsewhere (see below), this document places that literature in the context of the geographical, ecological, and cultural characteristics of the central Rocky Mountains. Similarly, this assessment emphasizes the biology, ecology, and status of Colorado River cutthroat trout with respect to the current environment. Nevertheless, it includes consideration of historical conditions deemed essential to understanding the evolutionary history and trajectory of this species, as well as those factors influencing the potential for future conservation.

Resources consulted for this assessment included the peer-reviewed literature, non-refereed publications, agency reports, and data from resource management agencies. Not all documents on Colorado River cutthroat trout are referenced in the assessment, nor are all materials considered equally reliable. The assessment gives greater credence to peer-reviewed literature because these publications have received formal scientific scrutiny. Less stringently reviewed materials and unpublished data were occasionally used when they were the best available information, but greater caution must be applied in their interpretation. Agency reports and expert opinion that were specific to particular waters were generally not included except when referring to Hirsch et al. (2006), who synthesized this information.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct critical experiments in the ecological sciences, and often observations, inference, logical thinking, and models must be relied on to guide the understanding of ecological relations (Hilborn and Mangel 1997). In this assessment, the strength of evidence for particular ideas is noted and alternative explanations are described where appropriate. Nonetheless, many of these explanations should be

regarded as working hypotheses until supported or refuted by scientific or management experiments.

Application and Interpretation Limits

Although salmonids are one of the best-studied groups of fishes in the world, cutthroat trout have not received attention comparable to that received by other taxa. For example, a search of the Aquatic Sciences and Fisheries Abstracts database (accessed 16 February 2006) revealed that since 1970, 390 peer-reviewed articles have appeared that include “cutthroat trout,” “*Oncorhynchus clarkii* (or *clarki*),” or “*Salmo clarki*” in the abstract. Over this same interval,

however, 944 articles have included the common or scientific name of brook trout (*Salvelinus fontinalis*), 1,848 have named brown trout (*Salmo trutta*), and 6,777 have named rainbow trout (*O. mykiss*). Studies of these nonnative species also appear to exceed those of the inland subspecies of cutthroat trout, even when the papers on brook, brown, and rainbow trout are restricted to Colorado, Wyoming, and Utah (**Figure 1**). This search located only 21 peer-reviewed papers on Colorado River cutthroat trout published since 1970. In addition, most populations of Colorado River cutthroat trout still extant in Region 2 are restricted to small headwater habitats, yet most research on cutthroat trout has focused on larger, migratory forms

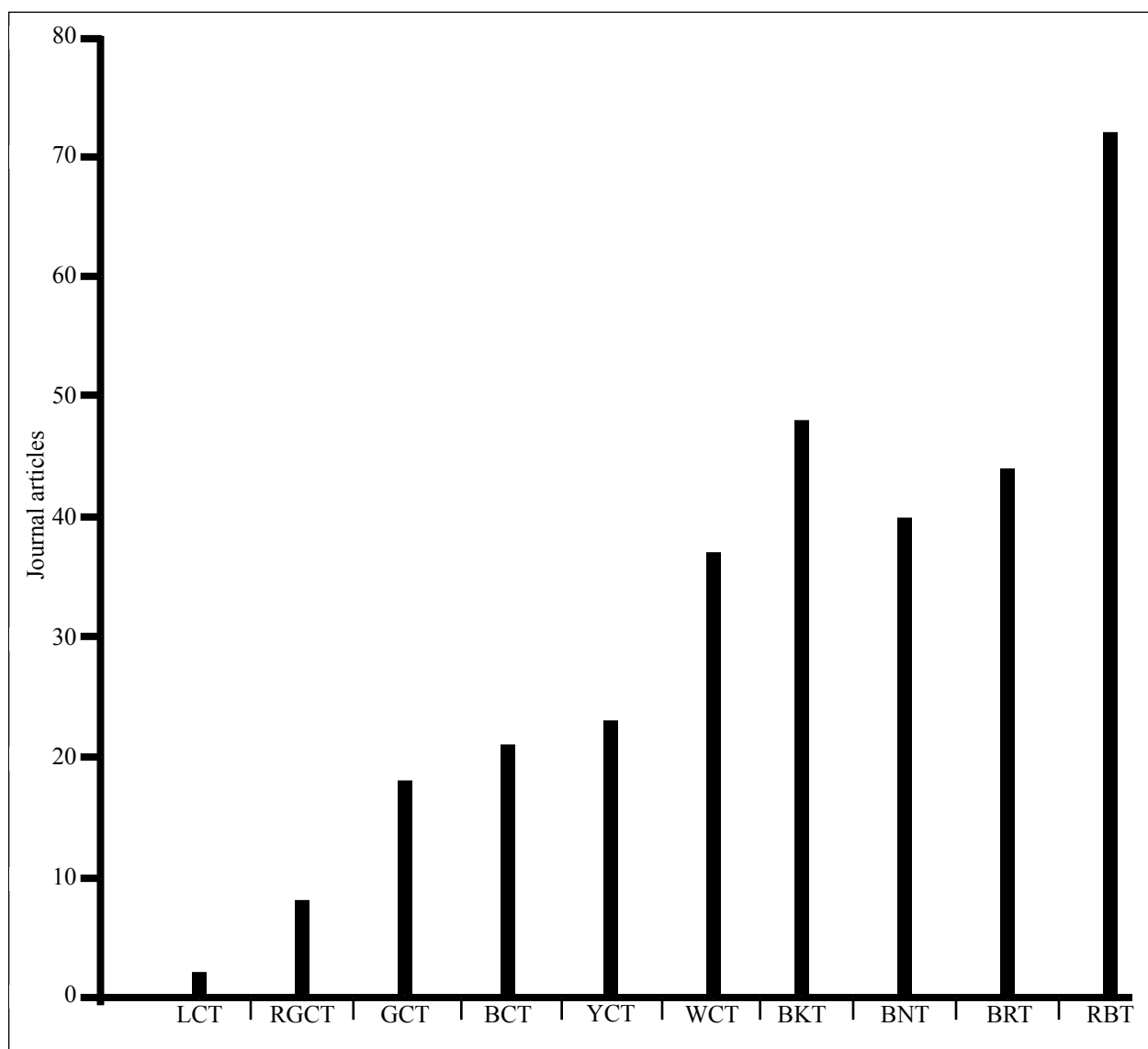


Figure 1. The number of peer-reviewed journal articles on subspecies of inland cutthroat trout and nonnative trout, based on a search of common and scientific names in the Aquatic Sciences and Fisheries Abstracts database on 16 February 2006.

of other subspecies. Thus, few conclusions about the biology, ecology, and management of Colorado River cutthroat trout can be drawn directly from published research and rely largely on syntheses of studies of related taxa, often in dissimilar environments, and on an understanding of salmonid biology as a whole. Consequently, I have generally been conservative in my interpretations, but urge the reader to recognize these limitations with respect to our knowledge of Colorado River cutthroat trout in Region 2 and to use caution in applying this information.

Publication on the World Wide Web

To facilitate the use of species assessments in the Species Conservation Project, they are being published on the Region 2 World Wide Web site (www.fs.fed.us/r2/projects/scp/assessments/index.shtml). Making documents available via the Internet makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, it facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer-reviewed prior to their release on the Web. This report was reviewed through a process administered by the American Fisheries Society, which chose a recognized expert (on this or related taxa) to provide critical input on the manuscript. Peer review was designed to improve the quality of communication and to increase the rigor and general management relevance of the assessment. A number of other individuals contributed their comments to earlier versions of this document; they are noted earlier in the acknowledgments.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Declines in the distribution of Colorado River cutthroat trout have prompted many agencies and organizations to recognize this subspecies as deserving of special management. The Colorado River cutthroat trout was first petitioned for listing as threatened or endangered under the Endangered Species Act in December 1999. In April 2004, the U.S. Fish and Wildlife Service (USFWS) issued its “90-day” ruling and concluded that this subspecies did not warrant listing (U.S. Fish and Wildlife Service 2004). In

September 2006, a federal judge ordered the USFWS to issue a 12-month finding of the status of this subspecies as specified under the Endangered Species Act. In June 2007, the USFWS (2007) again concluded that Colorado River cutthroat trout did not warrant listing. The USFS has designated the Colorado River cutthroat trout as a sensitive species in Regions 2 and 4. This subspecies is also on the Bureau of Land Management’s (BLM) Sensitive Species List, to which species are assigned because they “could easily become endangered or extinct in the state, including (a) species under status review by the FWS/ National Marine Fisheries Service, (b) species whose numbers are declining so rapidly that Federal listing may become necessary, (c) species with typically small or fragmented populations, and (d) species inhabiting specialized refugia or other unique habitats” (Bureau of Land Management 2002). The National Park Service does not afford this subspecies a special management designation. The Colorado Division of Wildlife lists it as a species of special concern. The Utah Division of Wildlife Resources has added the Colorado River cutthroat trout to its Sensitive Species List as a Conservation Species because a conservation agreement has been prepared for it (Utah Division of Wildlife Resources 2005). The Wyoming Game and Fish Department (Wyoming Game and Fish Commission 2001) has assigned it a Native Species Status of 2, indicating that populations are physically isolated or exist at extremely low densities throughout its range although habitat conditions appear to be stable. The American Fisheries Society considers the Colorado River cutthroat trout a species of special concern (Williams et al. 1989).

The Natural Heritage Program rank for cutthroat trout is G4 (global rank: uncommon but not rare; some cause for long-term concern due to declines or other factors) and for this subspecies is T3 (intraspecific rank: at moderate risk of extinction due to a restricted range, relatively few populations [often 80 or fewer], recent and widespread declines, or other factors). Within states, ranks are S3 (Colorado: vulnerable due to a restricted range, relatively few populations [often 80 or fewer], recent and widespread declines, or other factors making it vulnerable to extirpation), S2? (Utah: uncertain, but believed to be imperiled because of rarity due to very restricted range, very few populations [often 20 or fewer], steep declines, or other factors making it very vulnerable to extirpation), S1 (Wyoming: critically imperiled because of extreme rarity [often 5 or fewer occurrences] or because of some factor[s] such as very steep declines making it especially vulnerable to extirpation), and SX (New Mexico: extirpated) (NatureServe 2006). Note that the categorizations for

Colorado, Wyoming, and Utah do not reflect the current understanding of the distribution of this subspecies (Hirsch et al. 2006).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

All the national forests in Region 2 where Colorado River cutthroat trout historically occurred and are presently found – Arapaho-Roosevelt (Ficke et al. 2003), Grand Mesa-Uncompahgre-Gunnison (James 2003), Medicine Bow-Routt (Sealing et al. 1992, Speas et al. 1994), San Juan (Langlois et al. 1994), and White River (Sealing et al. 1992, Sanchez and Hirsch 2001) – have prepared management plans or assessments for this subspecies, sometimes in conjunction with the Colorado Division of Wildlife, Wyoming Game and Fish Department, or Bureau of Land Management. These management plans have been replaced by a rangewide conservation agreement and strategy that includes USFS Regions 2 and 4, the Colorado, Utah, and Wyoming state offices of the BLM, the USFWS, the Intermountain Region of the National Park Service, the Ute Indian Tribe in Utah, the Colorado Division of Wildlife, the Utah Division of Natural Resources, the Wyoming Game and Fish Department, and the state offices of Trout Unlimited in Colorado, Utah, and Wyoming (CRCT Conservation Team 2006a,b). The 5-year plan establishes general goals for the conservation and restoration of Colorado River cutthroat trout in portions of its historical range. Actions directed at achieving these goals include monitoring, protecting, improving, and where necessary isolating habitat; restricting harvest; establishing, monitoring, and surveying for populations; controlling and halting introductions of nonnative fishes and diseases; creating broodstocks; developing individual-basin management plans; and facilitating interagency cooperation and decision-making, as well as evaluating those decisions. This strategy is also likely to be incorporated in the Western Native Trout Initiative (<http://www.fishhabitat.org/documents/WNTIFactSheet.pdf>; D. Miller personal communication 2007) sponsored by a variety of state and federal agencies from the western U.S. whose objectives are to develop a common conservation strategy for native trout populations, streamline and prioritize efforts through information sharing, and better communicate their vision and accomplishments to the public and elected officials.

Biologists from many of these agencies also collaborated to produce a range-wide status assessment for Colorado River cutthroat trout (Hirsch et al. 2006),

largely following the protocol used for a similar assessment of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*; Shepard et al. 2005). This comprehensive assessment supersedes an earlier effort (Young et al. 1996), in particular providing much better data on this subspecies' distribution in Utah. It also provides the first map-based quantitative estimate of historical range, as well as addressing population size and connectivity, risks from nonnative fish, hybridization, and disease, the utility of waters as restoration sites, and many other factors. This compilation relied on a mix of published work, information from agency files and databases, and professional judgment. Thus the reliability of conclusions about particular waters varied greatly. Participants in this assessment intend to update these data annually and reanalyze them at 5-year intervals (CRCT Conservation Team 2006a).

In addition, many nongovernmental organizations have advocated for conservation of Colorado River cutthroat trout. A number of these groups – The Center for Biological Diversity, Biodiversity Legal Foundation, Biodiversity Associates, Ancient Forest Rescue, Southwest Trout, Wild Utah Forest Campaign, Center for Native Ecosystems, and Colorado Wild – petitioned this subspecies for federal listing under the Endangered Species Act. The Center for Biological Diversity, Biodiversity Conservation Alliance, Pacific Rivers Council, and Trout Unlimited also formed the short-lived Western Native Trout Campaign to promote restoration of healthy populations of nonanadromous salmonids in the western United States, primarily via participation in public processes associated with federal land and species management plans.

The Nature Conservancy, a national land trust whose mission is the preservation of biodiversity, has not targeted particular waters for the conservation of this subspecies. It is working on a large-scale initiative related to ecologically sustainable water management (Richter et al. 2003) and has crafted an ecoregional plan that specifies larger basins in which conservation may be a priority (Neely et al. 2001). Trout Unlimited, a national organization with state and local chapters dedicated to conservation of wild trout, has collaborated with a number of state and federal agencies and grassroots organizations to enhance and restore populations and to improve habitats in specific watersheds through their Embrace-a-Stream program. They also maintain public awareness via press releases, educational materials, and organizational initiatives. For example, Trout Unlimited is devising a Conservation Success Index to gauge the effectiveness of conservation measures for native trout and to prioritize future efforts.

Biology and Ecology

Systematics and general species description

The Colorado River cutthroat trout is in the order Salmoniformes and family Salmonidae. The genus *Oncorhynchus* in North America comprises cutthroat trout (until recently, *O. clarki*), rainbow trout, five species of Pacific salmon, Gila trout (*O. gilae gilae*), Apache trout (*O. g. apache*), Mexican golden trout (*O. chrysogaster*), Baja California rainbow trout (*O. mykiss nelsoni*), and several undescribed Mexican trout (Behnke 1992, Hendrickson et al. 2002). The Colorado River cutthroat trout is one of 14 subspecies of cutthroat trout in the western United States (Behnke 1992), some of which remain undescribed, may be of questionable validity, or represent a polyphyletic group with members warranting designation as individual subspecies (Martin et al. 1985).

The phylogenetic relationships among members of *Oncorhynchus* are poorly known and currently in dispute (Stearley and Smith 1993, Utter and Allendorf 1994, Oakley and Phillips 1999, Hendrickson et al. 2002). Behnke (1992) hypothesized that the major phylogenetic lines (i.e., coastal [*O. clarkii clarkii*], westslope, and Yellowstone cutthroat trout [*O. c. bouvieri*]) were probably established over one million years ago, after which an interbasin transfer from the upper Snake River to the upper Green River led to the spread of cutthroat trout in the Colorado River basin and the eventual evolution of Colorado River cutthroat trout. According to this perspective, glacial periods from 100,000 to 10,000 years ago resulted in stream captures from the Colorado River basin into the South Platte, Arkansas, and Rio Grande basins that led to the evolution of greenback cutthroat trout (*O. c. stomias*) and Rio Grande cutthroat trout (*O. c. virginalis*). In contrast, Smith et al. (2002; also see Minckley et al. 1986) proposed – based on mtDNA sequence divergence rates and fossil records – that the progenitor of cutthroat trout initially occupied waters of the Great Basin perhaps 8 million years ago, which it may have accessed by following the ancient course of the Snake River through southern Oregon, and began to differentiate into subspecies nearly 5 million years ago. This is in accordance with Stearley's (1992) hypothesized pre-Pleistocene occupation of Lake Lahontan by cutthroat trout. Smith et al. (2002) also argued for substantial connections among waters in the Great Basin, Colorado River, and Rio Grande from 9 million to 5 million years ago. Based on restriction fragment length polymorphisms of mitochondrial and ribosomal DNA, Dennis Shiozawa and Paul Evans

(personal communication 2007 and unpublished data) have hypothesized that a cutthroat trout exhibiting an archaic haplotype occupied habitats in all of these basins (as well as the South Platte and Arkansas River basins) and gave rise to Rio Grande, greenback, and Colorado River cutthroat trout, although the precise geographic and phylogenetic origins of each are uncertain. They also suggested that the structure of an additional haplotype in Colorado River cutthroat trout appears consistent with more recent evolutionary exposure to Yellowstone cutthroat trout, as Behnke (1992) suggested (also see A. Martin, J. Mitton, and J. Metcalf, University of Colorado, unpublished data). Although sampling has been limited, individuals with the archaic haplotype are uncommon in the northern portions of the historical range and could be restricted to isolated headwater habitats there, yet such fish may constitute the sole form present in the San Juan River basin. Only this presumptively older haplotype has been found in samples of greenback cutthroat trout and Rio Grande cutthroat trout, suggesting that their contact with Colorado River cutthroat trout had ceased prior to the latter's exposure to Yellowstone cutthroat trout. Metcalf et al. (In press) reported that the lineages leading to Colorado River cutthroat trout and greenback cutthroat trout diverged 0.7 to 2.0 million years ago, based on molecular clock estimates.

The Colorado River cutthroat trout is among the most colorful of the subspecies. Individuals display the light to deep red pigmentation of the gular folds that give the species its common name, as well as having black spots concentrated posteriorly and dorsally. The size and number of spots varies geographically, with spots tending to be fewer and larger in more southerly populations (Behnke 1992). The back is brownish or olivaceous, the sides paler and often with parr marks even in adult fish, and the belly is pale to light yellow (particularly in females) or melon orange to bright red (particularly in males). The opercula also exhibit these bright colors. Mature males display particularly intense coloration from autumn through the spawning season. Behnke (1992) and Baxter and Stone (1995) observed that this subspecies had 170 to 205+ scales in the lateral series, and 38 to 48+ scales above the lateral line, which were greater than counts in all other subspecies except greenback cutthroat trout.

Distinguishing Colorado River cutthroat trout from its two closest relatives can be difficult. Rio Grande cutthroat trout possess similar coloration, but they usually have fewer scales in and above the lateral line and more irregularly shaped spots on the caudal peduncle. Although greenback cutthroat trout tend to

have larger spots and more scales in and above the lateral line (Behnke and Benson 1980, Behnke 1992), there is substantial overlap in appearance with Colorado River cutthroat trout. Male greenback cutthroat trout in lakes are reputed to become a brighter shade of red during spawning, but male Colorado River cutthroat trout in similar habitats also adopt this appearance, which may be more of a reflection of the availability of carotenoid-containing prey (Putnam 1992) than of an inherent difference between subspecies. Even attempts to use genetic methods to discriminate between these subspecies have been unsuccessful (Leary et al. 1987, Kanda et al. 2002), but recent work with microsatellites (Metcalf et al. In press) has identified several diagnostic markers.

The two subspecies once were probably easily differentiated based on their distribution, but transbasin stocking has made this unreliable. Metcalf et al. (In press) discovered that several populations in the South Platte and Arkansas River basins that had been treated as greenback cutthroat trout were instead Colorado River cutthroat trout; these populations were probably established after 1896 when large numbers of Colorado River cutthroat trout were introduced on both sides of the Continental Divide (W. Wiltzius, Colorado Division of Wildlife, unpublished data). Ironically, at least one putatively pure population of Colorado River cutthroat trout in the upper Colorado River basin is actually greenback cutthroat trout. These apparently originated from plants before 1896, but it is uncertain whether they were derived from the South Platte or Arkansas River basin. Because individuals from some of the populations noted above were used in earlier taxonomic assessments, there may be less overlap in morphological and genetic characteristics between subspecies than previously assumed. Regardless, the taxonomic relations among greenback cutthroat trout, Rio Grande cutthroat trout, and the presumptively archaic and recent forms of Colorado River cutthroat trout merit continued investigation (also see Behnke 1979; J. Metcalf and A. Martin, University of Colorado, unpublished data).

Distribution and abundance

For the purposes of this assessment, I consider the historical range of Colorado River cutthroat trout to include the colder waters of the Colorado River basin above the Grand Canyon, primarily in Colorado, Utah, and Wyoming (**Figure 2**). As noted earlier, this distribution probably resulted from the

arrival and spread of a cutthroat trout from the Great Basin via ancient major river connections or relatively contemporaneous headwater transfers (Minckley et al. 1986, Smith et al. 2002).

Subsequent climatic and geological events within the Colorado River basin further delimited this range. The last glacial maximum in the Rocky Mountains was about 29,000 to 23,000 years ago with rapid recession of these glaciers 18,000 to 17,000 years ago throughout the central and southern Rockies (Menounos and Reasoner 1997, Licciardi et al. 2004, Pierce 2004, Benson et al. 2005). Glacial Lake Bonneville, which covered about one-third of what is presently the state of Utah, appears to have enhanced local precipitation sufficiently to delay glacial retreat in the Uinta Mountains and Wasatch Range for up to 2,000 years (Munroe et al. 2006). Thereafter, a modest glacial advance 13,000 to 11,000 years ago during the Younger Dryas period formed and filled additional glacial cirques in the mountains of Colorado and Wyoming (Menounos and Reasoner 1997, Licciardi et al. 2004, Pierce 2004). During cold periods, large valley glaciers 200 to 450 m thick were common in the higher mountain ranges in Colorado, and their lower termini often extended downslope to elevations of 2,200 to 2,700 m (Madole 1976, Madole et al. 1998). The snowline was also 600 to 1,000 m lower than at present, and portions of southern Wyoming, such as at or near the present locations of Green River, Rawlins, Laramie, and Cheyenne, were subject to permafrost (Mears 1987, 2001; Whitlock et al. 2002). Average summer temperatures may also have been 10 to 15 °C below those presently observed (Mears 1987, Pierce 2004). These glacial periods would have prevented fish from occupying nearly all high-elevation lakes and headwater streams, and displaced them downstream into larger, warmer waters. The ensuing warming and melting, in which mean annual temperatures may have risen 7 to 10 °C in less than 20 years (Whitlock et al. 2002), marked the end of transbasin movements via stream capture, but also permitted reoccupation of streams that were previously too cold for successful recruitment. Nevertheless, the glacial legacy of steep channels and hanging valleys limited later colonization of many of these sites, as did two additional processes. First, mountain landscapes have been undergoing isostatic rebound in response to the declining mass of ice (a process which can be surprisingly swift; Watts 2001, Clague and James 2002), with different faults rising at different rates (Hetzl and Hampel 2006) leading to nickpoints in stream profiles. Second, streams have been differentially downcutting

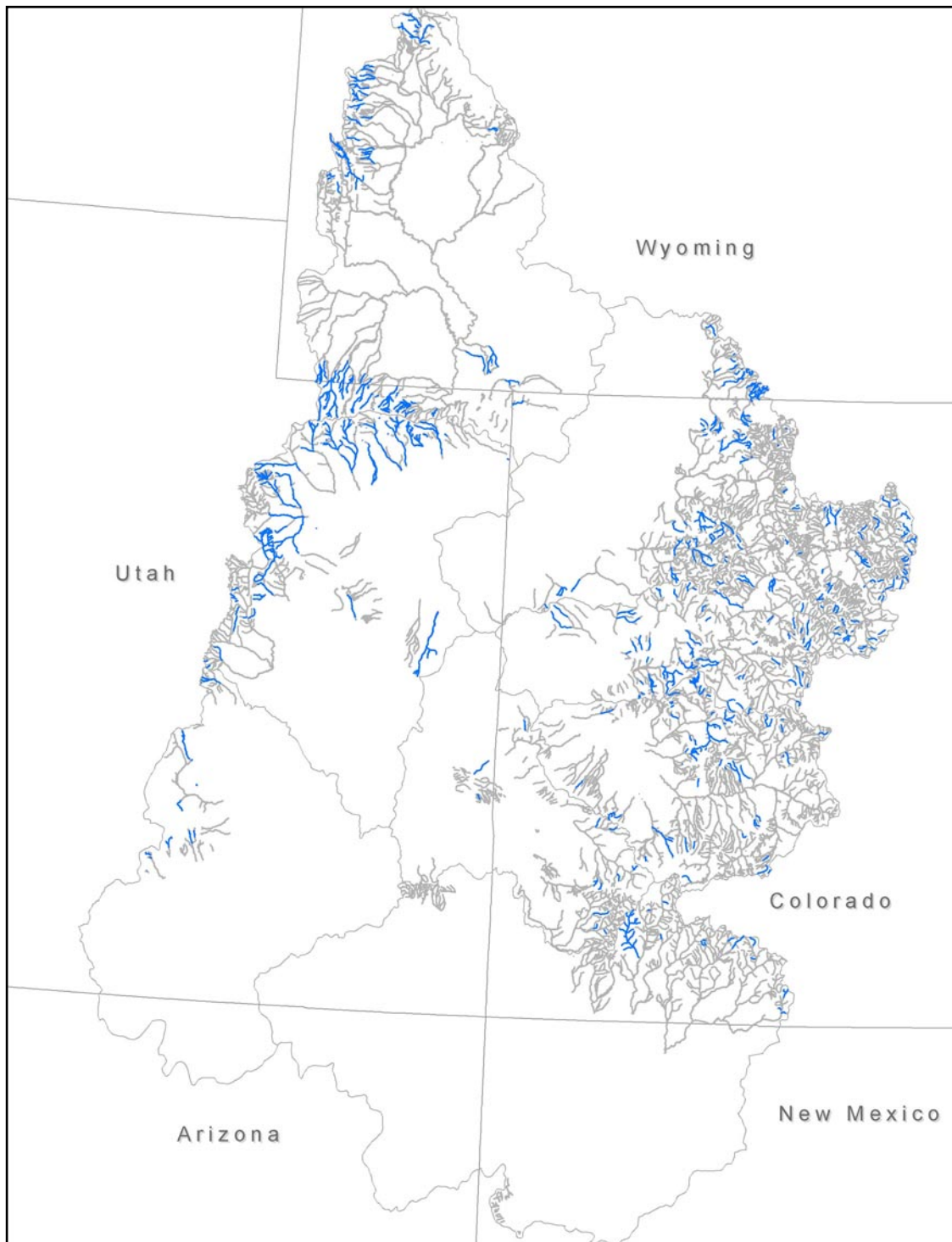


Figure 2. The current (blue) and historical (gray) range of Colorado River cutthroat trout, based on expert opinion. From Hirsch et al. (2006).

through resistant and nonresistant rock in response to reduced sediment availability since deglaciation. Together, these processes are likely to have produced many of the geological barriers to fish movement that are currently present as well as isolating some extant

indigenous populations (for comparable examples with other salmonids, see Berg 1985, Castric et al. 2001).

Processes over shorter timescales have also altered the distribution of Colorado River cutthroat

trout. Climate cycles at intervals of decades to centuries, exemplified by the El Niño/Southern Oscillation and the Pacific Decadal Oscillation and driven in part by irregularities in the earth's orbit around the sun (Mantua et al. 1997, Whitlock et al. 2002, Hessburg et al. 2005), have probably led to repeated extinctions, but headwater refugia during droughts and main-stem river or low-elevation lake refugia during wetter periods facilitated recolonization of accessible waters. Similarly, fire-related debris flows or storm-related mass failures may have eliminated or isolated some populations of Colorado River cutthroat trout, and barrier failure and fish migration may have restored this subspecies to some waters. Consequently, the historical range noted earlier represents a snapshot in time of the complex interplay between climate, geology, and disturbance, and the evolutionary history, demographic resilience, and dispersal ability of Colorado River cutthroat trout.

The majority of suitable habitats within modern times has included headwater tributaries, larger streams, and portions of main-stem rivers. Glacial advances and retreats probably rendered all but a few lakes (e.g., Trappers Lake in northwestern Colorado and the Green River Lakes in northwestern Wyoming) inhospitable or inaccessible to Colorado River cutthroat trout (cf. Bahls 1992, Bowman et al. 2002). Their current presence in most lakes is a result of fish stocking over the last century (Young et al. 1996).

The loss and anthropogenic transfer of populations began long before the range of this species was described, so our knowledge of historically occupied locations is at best approximate. Hirsch et al. (2006) defined historical fluvial habitat primarily as those accessible streams above an elevation of 1,829 m (1,676 m for streams flowing north), and they concluded that about 34,500 km of streams were historically occupied and about 22,500 km of those were in Colorado and that portion of Wyoming in Region 2 (this includes lands administered by federal or state agencies and on private land). Nevertheless, the downstream limits of Colorado River cutthroat trout may have been lower and the occupied range greater. Accounts from the late 1800's and early 1900's note that fish in rivers such as the Green, Yampa, Gunnison, San Juan, and Colorado were both abundant and large (Wiltzius 1985, Behnke 1992, Smith et al. 2002). Historical accounts of the downstream limits of other subspecies in similar basins (e.g., greenback cutthroat trout in the South Platte River near the site of Greeley, Colorado [Wiltzius 1985] or westslope cutthroat trout below the Great Falls of the Missouri River, and the present lower elevational limits of Lahontan cutthroat trout [*Oncorhynchus*

clarkii henshawi] of 1,650 to 1,950 m [Dunham et al. 1997]) imply that Colorado River cutthroat trout were also probably observed well downstream from current elevational limits. In addition, portions of main-stem rivers that are regarded as uninhabitable by trout because of high turbidity or warm summer temperatures may have been used seasonally or for overwintering (cf. Clapp et al. 1990), particularly in those basins in which modern land uses have contributed to habitat degradation. Finally, it is also likely that there were latitudinal clines in the downstream distribution of Colorado River cutthroat trout related to water temperature (Dunham et al. 1999).

Overall, there is consensus that the distribution of Colorado River cutthroat trout has dramatically declined since the mid-1800's. Behnke and Benson (1980), Behnke (1992), and Young et al. (1996) estimated that this subspecies occupied perhaps 1 to 5 percent of its historical range, but they did not quantitatively estimate the size of that range. Young et al. (1996) based this estimate on the distribution of indigenous, allopatric, genetically pure populations. The recent status assessment for Colorado River cutthroat trout (Hirsch et al. 2006) differentiates among core conservation populations, which are believed to be genetically unadulterated; conservation populations, which carry a small proportion of nonnative genes but exhibit unique life histories or phenotypic characteristics; and populations of lesser genetic integrity and ecological value (Utah Division of Wildlife Resources 2000). Collectively, both types of conservation populations are thought to occupy 8 percent (2,900 km) of their historical fluvial range; including the third group raises this total to 13 percent (about 4,850 km, of which 1,650 km are on lands administered by Region 2).

Population trend

Present trends in the number and size of populations are difficult to gauge because not all extant populations have been monitored over the past several decades, large fluctuations in abundance may be typical (Platts and Nelson 1988), and what is known indicates that the total number and size of populations remains in flux. The loss or introgression of populations from invasions of nonnative trout is ongoing (Behnke 1992, Peterson and Fausch 2003, Wyoming Game and Fish Department, unpublished data), and drought early in the 21st century may have eliminated populations from small streams in some areas (Brauch and Hebein 2003, Wyoming Game and Fish Department, unpublished data). Current or former land management activities (e.g., livestock grazing or road construction) may be

depressing some populations, but these effects are difficult to quantify (Shepard et al. 2005). Nevertheless, the increased awareness of the status of this subspecies and increased agency conservation efforts since the 1970's have apparently arrested the rapid loss of known populations. Populations have been restored to portions of streams after the removal of nonnative fish species, with the objective of establishing connectivity among populations in some areas (e.g., the West Branch and main-stem North Fork Little Snake River, Wyoming and the South Fork Little Snake River, Colorado). These activities increased the occupied range of Colorado River cutthroat trout by over 150 km from 1999 to 2003 (CRCT Coordination Team 2005). In addition, recent surveys of streams for populations, as well as more comprehensive genetic testing of existing populations, increased the estimated occupied habitat by over 600 km between 1999 and 2003 (CRCT Coordination Team 2005). Consequently, the risk of extinction of this subspecies is less than previously thought, but many individual populations remain at a relatively high risk of extirpation because of the potential for replacement by nonnative trout (Hirsch et al. 2006). Also, the absence of this species from rivers and most larger streams with apparently suitable habitat implies that the average size of populations has decreased from historical norms (cf. Young et al. 2005); over 50 percent of occupied streams have average widths less than 3.3 m (about 2 percent exceed 7.5 m) and half of those containing conservation or core conservation populations are less than 6.0 km (Hirsch et al. 2006).

Activity pattern and movements

The last two decades have seen a paradigmatic shift in our beliefs about movement of salmonids in streams. Previously, most stream fishes, among them cutthroat trout, were believed to complete their entire life cycle in short stream reaches or in just a single pool (Funk 1957, Miller 1957, Gerking 1959). This conclusion, however, was partly a result of the methodology used to study movement. Typically, these studies relied on sampling and marking fish annually within the same relatively short reaches. When resampled, the majority of marked fish that were recovered were found in the same location in which they had been marked, which led investigators to conclude that most stream fish did not move long distances. However, a very small proportion of the marked fish were generally recaptured, and sample reaches usually represented a tiny fraction of all available habitat (Gowan et al. 1994, Albanese et al. 2003). With the advent of radiotelemetry (Clapp et al. 1990), simple two-way traps (Gowan and Fausch 1996), individually recognizable tags (e.g.,

passive integrated transponder tags; Braennaes et al. 1994), sophisticated genetic techniques (Neville et al. 2006b), and elemental analyses of bony structures (Rieman et al. 1994), researchers have begun to portray a more comprehensive picture of the role of movement in the life histories of stream fishes. While several of these studies have examined cutthroat trout, few have been specific to Colorado River cutthroat trout. The inferences below are drawn from studies of the movements of several salmonid species and are believed to represent those historically or currently undertaken by Colorado River cutthroat trout.

Territoriality

Like many salmonids, cutthroat trout often become territorial and defend a foraging space from competitively subordinate (usually smaller) fish (Nakano et al. 1998, Gowan and Fausch 2002). Within territorially-structured populations, dominant individuals occupy the most bioenergetically favorable positions, such as the head of a pool, with subordinate fish likely to be downstream and to either side in less optimal sites (Lewynsky 1986, Hughes 1992). Such structuring might be regarded as antithetical to notions of mobility, but territory size is plastic and compresses when food is abundant (Chapman 1966). Furthermore, dominant individuals may occupy particular sites only until bioenergetic demands exceed available resources, and then move in search of new sites offering greater returns (Gowan and Fausch 2002, Gowan 2007). Conversely, when resources are less predictable in time and space (e.g., the punctuated streamside inputs of terrestrial macroinvertebrates), different positions are bioenergetically equivalent (e.g., locations within beaver ponds), or food can be rapidly depleted (e.g., forage fish), then territoriality may break down completely with fish forming less spatially stable dominance hierarchies or adopting individual "floater" strategies. Territorial dominance, subordination, and floating may exist simultaneously among different individuals in a single system (Nielsen 1992). Territoriality may also dissolve when fish occupy positions for reasons other than foraging, as in the winter aggregations of cutthroat trout in pools (Jakober et al. 1998).

Diel movements

Studies of movement patterns of cutthroat trout at short temporal scales of hours to a day are rare, and the results may be more of a reflection of the seasons and habitats evaluated than of the actual diversity in movement over this interval. Young et al. (1997a) examined the hourly positions of Colorado River

cutthroat trout for six, 24-h cycles from mid-July to late August in the North Fork Little Snake River in Wyoming. They found that median distances traveled during the diel cycle varied from 27 to 90 m and declined over the summer, whereas home ranges were smaller (median <27 m) and did not show a statistically significant decline with time. The study also revealed that Colorado River cutthroat trout were most active during the day, less so during crepuscular periods, and largely inactive at night; however, changes in position were unrelated to time of day. Bonneville cutthroat trout *Oncorhynchus clarkii utah* had comparable summer diel home ranges, with peaks in movement at dawn and dusk (Hilderbrand and Kershner 2000). Schmetterling and Adams (2004) found that subadult westslope cutthroat trout tended to move at night in summer, which has been reported for other juvenile salmonids during outmigrations (Jonsson and Antonsson 2005). Other trout species, studied in larger systems, have displayed more extensive movements and alternate activity patterns that may in part reflect different foraging strategies (e.g., piscivory) (Young et al. 1997b, Young 1999).

Diel movements have also been examined in winter, typically in association with changes in position in the water column rather than location within a stream. During winter, individuals small enough to conceal within the stream substrate will do so during the day, and re-emerge at night (Vore 1993, Bonneau and Scarnecchia 1998). Larger fish sometimes congregate in pools during the day, and move to shallower, moving waters at night (Harvey et al. 1999, Jakober et al. 2000). This diel shift is thought to be in response to an increased vulnerability to diurnal predators caused by a reduction in swimming burst speed at very cold temperatures (Jakober et al. 2000). This behavior is common to many species of salmonids and has been observed in summer when water temperatures decline below 10 °C (Hillman et al. 1992, Thurow et al. 2006).

Seasonal movements

Spawning migrations often constitute the most dramatic movements made by salmonids, but movements associated with seasonal changes may also be substantial. Schmetterling and Adams (2004) observed that 14 to 48 percent of westslope cutthroat trout in different segments of a 2nd-order stream moved during a 3-week interval in mid-summer, and the median distance traveled by mobile fish was 91 m. Young (1996) observed that Colorado River cutthroat trout occupied summer home ranges of 11 to 652 m (median, 45 m) in a 3rd-order Wyoming stream and

that weekly movement declined as summer progressed (also see Young et al. 1997a, Hilderbrand and Kershner 2000). Fluvial Bonneville cutthroat trout in tributaries of a large basin also occupied summer home ranges under 300 m (Schrack and Rahel 2004, 2006). Increases in abundance of Colorado River cutthroat trout in two streams as flows declined from July to August also implied that these fish moved during summer (Herger et al. 1996).

Declining temperatures in autumn appear to trigger substantial movements in many populations of cutthroat trout. Fluvial westslope cutthroat trout in tributaries to the Middle Fork Salmon River in September and October moved downstream an average of 91 km by the following February (Zurstadt and Stephan 2004), whereas movements of fish with a resident life history or occupying smaller basins have been shorter (Brown and Mackay 1995b, Jakober et al. 1998, Lindstrom 2003). For example, Brown (1999) observed that about half of the westslope cutthroat trout radio-tagged in August had moved on average 1.0 km as temperatures declined to 3 to 4 °C in late October, and that all fish had moved by late November when temperatures approached 0 °C. Thereafter, many of these fish aggregated in deep pools and ceased further movement, but some fish again moved a comparable distance apparently after being displaced by anchor ice (also see Lindstrom 2003). In contrast, Colorado River cutthroat trout in the headwaters of the North Fork Little Snake River in Wyoming did not alter their positions during the summer-autumn transition (Young 1998).

Although mid-winter movements in small streams with ice or snow cover tend to be limited (Chisholm et al. 1987, Brown 1999, Hilderbrand and Kershner 2000), movements in larger systems can be substantial. Colyer et al. (2005) reported that fluvial Bonneville cutthroat trout occupied average home ranges of 300 and 1,900 m in two years in a river main stem during winter where warmer water temperatures (2 to 4 °C) may have permitted continued foraging and growth.

Life-history-related movements

Most spawning movements in cutthroat trout are initiated as flows increase in spring or early summer, with the peak often coinciding with annual peak flow (Benson 1960, Bernard and Israelsen 1982, Schmetterling 2001, Zurstadt and Stephan 2004). Adults usually remain in the spawning streams for a fairly brief period (e.g., 2-19 d, Brown and Mackay 1995a; 9-11 d, Magee et al. 1996; 22-52 d, Schmetterling 2001; 17 d, De Rito 2004) before

departing back to summer growth sites. The magnitude of pre- and post-spawning migrations greatly varies and probably is dictated by stream connectivity. Young (1996) reported that post-spawning migrations (and by inference, pre-spawning migrations) for small (<250 mm total length) Colorado River cutthroat trout in an isolated 3rd-order stream were up to 1.8 km. Brown and Mackay (1995a) observed that spawning westslope cutthroat trout (median fork length 330 mm) above a fish barrier moved a median of 3.5 km to spawning sites and 2.4 km on return migrations. In contrast, cutthroat trout with unimpeded access to larger waters moved extensively. Westslope cutthroat trout migrated 2 to 72 km up the Blackfoot River on spawning runs (Schmetterling 2001) and Yellowstone cutthroat trout in the Yellowstone River moved 1 to 53 km to tributaries to spawn (Clancy 1988). Large (236 to 503 mm total length) Bonneville cutthroat trout with access to the main-stem Bear River or its major tributaries, the Smiths Fork and Thomas Fork, moved 0.5 to 86.0 km (Schrack and Rahel 2004, Colyer et al. 2005).

Following emergence from spawning substrates, cutthroat trout fry shift to nearby shallow, low-velocity habitats (Moore and Gregory 1988, Bozek and Rahel 1991b). Thereafter, however, the few studies on movements of cutthroat trout fry indicate that they can be quite mobile, particularly the offspring of fluvial or adfluvial forms (Northcote 1992). Benson (1960) noted that in a Yellowstone Lake tributary, fry emerged about 30 days after depositing their eggs, and their outmigration to the lake peaked in late July and ended by late October. Nearly 90 percent of all outmigrants were recently emerged fry, and the remainder were age 1 or 2 (also see Gresswell et al. 1994, 1997). Snyder and Tanner (1960) and Drummond (1966) observed comparable patterns for Colorado River cutthroat trout fry in tributaries to Trappers Lake in Colorado; they also noted that these migrations were nocturnal. Recently emerged Bonneville cutthroat trout left their natal stream from August to November to overwinter in a river main stem (Bernard and Israelsen 1982). Not all studies, however, have indicated that fry migrate shortly after emergence. For example, Young and Guenther-Gloss (2004) demonstrated spatial differences in abundance of adult and age-1 greenback cutthroat trout in South Platte River tributaries, which implied that movements of many juveniles were delayed until at least 1 year after emergence, although the timing of these movements was unknown. Westslope cutthroat trout juveniles reared for up to 3 years in streams before migrating to main-stem rivers (Schmetterling 2001), a pattern similar to that observed for Colorado River cutthroat trout in tributaries to the North Fork Little Snake River (M.K.

Young, unpublished data). Late summer sampling in that basin failed to detect substantial downstream movements of juveniles (Jespersen 1981, M.K. Young, unpublished data), and it is assumed that outmigrations are concomitant with high spring flows.

In summary, it is evident that cutthroat trout life histories are characterized by movements of many life stages in many seasons. The ubiquity of movement probably applied historically to Colorado River cutthroat trout, and may characterize the behavior of some extant populations. Moreover, it is important to note that lack of movement within a particular season or life history stage is not conclusive evidence of a sedentary life history strategy. Monitoring at annual intervals has demonstrated that fish do not necessarily show high fidelity to positions they have previously occupied. Bjornn and Mallet (1964) marked westslope cutthroat trout along a 120-km reach of the Middle Fork Salmon River from June to October, and resampled this reach annually for three years. Over 65 percent of fish were recaptured over 3 km from where originally found, and over 40 percent were more than 16 km away (also see Zurstadt and Stephan 2004). After a year, nearly 40 percent of marked Bonneville cutthroat trout in a much smaller stream were recaptured 331 to 3,292 m from where they were initially caught (Hilderbrand and Kershner 2000). Similarly, a 5-year study of Colorado River cutthroat trout in the North Fork Little Snake River basin revealed that at least 40 percent of marked fish occupied new locations in different summers, with between-year changes in location of up to 7.5 km (M.K. Young, unpublished data).

Finally, directionality in movements cannot be assumed. Cutthroat trout in some large river systems consistently moved downstream after spawning (Bjornn and Mallet 1964, Schrank and Rahel 2004, Zurstadt and Stephan 2004). Elsewhere, however, individuals in both small and large basins moved up- or downstream after spawning (Clancy 1988, Brown and Mackay 1995a, Young 1996, Hilderbrand and Kershner 2000, Schmetterling 2001) and during fall and winter (Brown and Mackay 1995b, Brown 1999, Lindstrom 2003).

Habitat

Colorado River cutthroat trout have occupied relatively steep, coldwater streams and rivers and accessible high-mountain lakes in the Colorado River basin for millennia. Their habitat use resembles that of other salmonid fishes in mountain environments, and probably reflects a shared evolutionary history. Some aspects of habitat use (e.g., spawning habitat and

juvenile habitat) have been addressed elsewhere in this document; the following discussion highlights a few additional elements of this well-studied subject.

Temperature

Cutthroat trout, like all salmonids, are ectothermic; water temperature drives many physiological processes and thus dictates the suitability of habitats. Although it is well known that trout mortality can be severe at very high water temperatures, the designation of biologically meaningful temperature maxima has varied depending on the method used. For example, using constant temperatures, Bear (2005) found that 50 percent of westslope cutthroat trout had died after 60 days at 19.6 °C. Johnstone and Rahel (2003) used laboratory experiments to identify 24.2 °C as the 7-day upper incipient lethal temperature for Bonneville cutthroat trout when temperatures were held constant, and they noted that environments cycling between 16 and 26 °C were not fatal but induced sublethal effects. These effects include a decline or halt in feeding and growth and the appearance of heat stress proteins at temperatures above 22 to 24 °C (Dickerson and Vinyard 1999, Meeuwig et al. 2004). Nonetheless, field observations indicate that cutthroat trout occupy waters that temporarily exceed these thresholds. Schrank et al. (2003) reported that Bonneville cutthroat trout apparently experienced maximum daily temperatures of 27 °C in a western Wyoming stream, and these fish neither died nor moved. They regarded the relatively short period that temperatures remained this warm, as well as the large diel fluctuations in temperature, as mitigating possible lethal effects (also see Dunham et al. 2003a).

Many populations of cutthroat trout are exposed to very cold water temperatures (near 0 °C) during winter. This does not represent a substantial physiological challenge for most age-1 and older fish, but that is not the case for fry that emerged during the previous growing season (Cunjak and Power 1987). It is the average summer temperature, however, that dictates the risk of winter mortality through its effects on the duration of incubation and period of post-emergence growth. If cutthroat trout fry have not grown sufficiently in the interval between emergence and the onset of cold winter temperatures (<4.0 °C), mortality rates are generally high (Coleman and Fausch 2007a) and may be related to recruitment failures observed in several streams (Harig and Fausch 2002, Peterson 2002, Coleman and Fausch 2007b). A similar pattern has been observed for brown trout at high latitudes in Scandinavia (Borgström and Museth 2005). For Colorado streams, the probability of

successful establishment of populations of greenback cutthroat trout or Rio Grande cutthroat trout was predicted in part by mean July water temperature, with successes associated with streams above 7.1 °C (Harig and Fausch 2002). Additional field and laboratory studies confirm that this summer temperature threshold is between 7.0 and 8.5 °C, or a threshold of about 900 degree-days during the growing season (Coleman and Fausch 2007a,b).

Optimal temperatures for growth fall between these two extremes. Bear (2005) determined that growth rates of westslope cutthroat trout peaked at a constant temperature of 13.6 °C (see Meeuwig et al. 2004 for similar results with Lahontan cutthroat trout). Similarly, the scope for activity, a measure of the oxygen physiologically available to an individual fish, peaked near 15 °C (Dwyer and Kramer 1975). These laboratory studies of individual growth and survival, however, require field validation and can be informed by an appreciation of the population-scale effects of water temperature. For example, westslope cutthroat trout tended to occupy tributaries to the Madison River in Montana that had average summer temperatures below 12 °C and maximum average summer temperatures below 16 °C (Sloat et al. 2002). Similarly, Isaak and Hubert (2004) found that abundance of trout, including cutthroat trout, in the Salt River basin of western Wyoming and eastern Idaho peaked at mean summer water temperatures of 12 °C and declined at warmer or cooler temperatures. This dome-shaped pattern probably applies in general to Colorado River cutthroat trout, but optimal temperatures may vary with other habitat conditions.

Channel units and structure

The importance of pools to salmonids has long been recognized, and Colorado River cutthroat trout are not exceptional in this regard; they disproportionately used pools relative to riffles during summer observations (Young 1996, Young et al. 1997a). As daytime foraging sites, the heads of pools usually provide the greatest energetic returns at the least cost in small to medium-sized streams (Hughes 1992, Gowan and Fausch 2002) because macroinvertebrate production in upstream riffles is often high and has not been cropped by other fish and the reduced velocity in pools requires less energy for fish to maintain position. It should be noted, however, that adult cutthroat trout do not solely occupy pools. Adult Colorado River cutthroat trout were found to move through up to five habitat units over a single 24-hour period in summer, and activity patterns suggested they were feeding in all habitats (Young et al. 1997a).

Furthermore, when introduced into long reaches of a fairly large stream from which all dominant competitors had been removed, individual Colorado River cutthroat trout disproportionately, but not exclusively, chose to inhabit pools (Young et al. 1998). Many occupied sites within riffles provided pool-like habitats (M.K. Young, personal observation), suggesting that the scale at which cutthroat trout select habitats could decouple the perceived relation between pools and fish abundance (see Spatial patterns and temporal dynamics, below).

In mid-winter, deep pools or those with surface ice are oft-used habitats, as are beaver ponds or portions of streams receiving warmer groundwater (Chisholm et al. 1987, Brown and Mackay 1995b, Jakober et al. 1998, Lindstrom 2003). These habitats minimize bioenergetic expenditures, provide security from predators during the day, and may be the most stable habitats under varying ice conditions, such as when frazil and anchor ice form during the supercooling of surface water exposed to the sky (Brown 1999). The severity of winter conditions and need for these habitats can vary with respect to the longitudinal position of fish in a stream. For example, in the Snowy Range in southeastern Wyoming, deep snow above 2,900 m prevented ice formation over streams whereas surface ice completely covered them below 2,500 m. At intermediate elevations, streams exhibited a mix of snow cover, surface ice, and open water, with the latter periodically influenced by anchor ice; such locations may represent the most extreme winter conditions for salmonids (Chisholm et al. 1987). Similar instability may develop in areas downstream from groundwater sources (Lindstrom 2003).

Channel properties also influence the abundance and production of cutthroat trout. Platts (1979) noted that cutthroat trout appeared to reach their highest densities in 2nd - to 4th-order streams, which afford the habitats most suitable for spawning and juvenile rearing. These sites also may be more productive because of the relatively high allochthonous inputs, such as terrestrial macroinvertebrates and litter, from riparian zones (Vannote et al. 1980, Baxter et al. 2005). Several studies have indicated that there is a minimum threshold in stream size below which cutthroat trout presence is unlikely (Kruse et al. 1997, Dunham et al. 2002b, Harig and Fausch 2002).

In general, cutthroat trout appear to occupy higher-gradient sites than other trout species in many Rocky Mountain streams (Fausch 1989, Bozek and Hubert 1992), and it has been suggested that these represent the most suitable reaches for cutthroat trout (Griffith 1988). More likely, however, is that nonnative

trout are largely excluding cutthroat trout from lower-elevation, lower-gradient stream segments, and that the steep, high-elevation habitats are the least suitable for nonnative species or are more likely to contain fish migration barriers, permitting cutthroat trout to persist there (Fausch 1989). A sampling scheme that corrected for the covariation between gradient and elevation revealed that gradient had little effect on trout biomass in Wyoming and Idaho streams (Isaak and Hubert 2000).

Cover and complexity

Despite that the presence of cover reduces the feeding efficiency of cutthroat trout, cover is thought to represent one of the most fundamental habitat needs of salmonids in streams (Wilzbach and Hall 1985, Wilzbach et al. 1986). Its primary role appears to be as a sanctuary from predators (Helfman 1981), but it may also offer shelter from high flows (Harvey 1998, Harvey et al. 1999). Yet because many habitat elements can serve as cover (e.g., large wood, overhanging or submerged vegetation, roots of bankside trees and shrubs, beaver dams, rubble and boulders, deep or turbulent water, or undercut banks), it may rarely be limiting in unaltered streams. Perhaps for this reason, Young (1996) found no difference in the proximity to cover of sites used by and available to Colorado River cutthroat trout. More critical may be the hydraulic and physical complexity of channels that generates an array of microsites. Channel complexity has been related to the density of Colorado River cutthroat trout (Kershner et al. 1997). Although a number of geomorphic elements can influence complexity (e.g., boulders, Warren and Kraft 2003; streamside vegetation, Kershner et al. 1997), large wood (also known as coarse woody debris) plays a dominant role in many montane streams where Colorado River cutthroat trout persist. Deposition of large wood affects sediment scour and deposition, energy dissipation, and channel form (Montgomery et al. 2003), and creates pools, stores spawning gravels, affords overhead cover, and provides refuge during high flows (Dolloff and Warren 2003). For Colorado River cutthroat trout in a Wyoming stream, pools formed by large wood were disproportionately occupied relative to other pool types (Young 1996). Removals or additions of large wood have caused declines or increases in local salmonid abundance (Dolloff 1986, Bisson et al. 2003).

A variety of processes control the inputs of large wood. Mass mortality of riparian stands from fire, insect damage, or wind are important sources (Veblen et al. 1994, Bragg 2000), as well as individual treefall from bank undercutting or self-thinning or pulsed

contributions from landslides or debris torrents (Cannon 1999, May and Gresswell 2003, Reeves et al. 2003b). Large wood abundance is characterized by high spatial and temporal variability among and within streams in the Rocky Mountains (Richmond and Fausch 1995, Hauer et al. 1999, Young et al. 2006), and it is hypothesized to loosely track forest succession and snag availability, with large wood loads peaking shortly after disturbance and during the old-growth phase (Minshall and Brock 1991, Bragg et al. 2000, Gregory et al. 2003).

Spatial patterns and temporal dynamics

The preceding paragraphs noted an array of habitat features that may be needed to sustain cutthroat trout populations. Although a number of models have been developed that relate habitat to trout abundance in small streams (e.g., Hickman and Raleigh 1982, Clarkson and Wilson 1995), these models often perform poorly, particularly when applied outside the systems for which they were developed (Fausch et al. 1988). Although this flaw is to some degree inherent to habitat models, their imprecision also arises from neglecting the spatial context of habitats, whether within the sampled reaches, between adjacent reaches, or among tributaries within a basin (Fausch et al. 2002). Dunning et al. (1992) introduced four concepts useful in evaluating how the abundance and distribution of habitats affects population size and persistence: habitat complementation, habitat supplementation, source-sink structure, and neighborhood effects. Habitat complementation refers to the spatial distribution of essential habitats that are not substitutable (e.g., spawning gravels, foraging sites, and overwintering refuges). Habitat supplementation deals with substitutable habitats, such as a feeding site for obtaining drift and a feeding site for exploiting terrestrial infauna. Source-sink structure refers to the demographic support provided by those areas that produce a surplus of individuals to areas in which populations may not be sustainable. Neighborhood effects involve how adjacent habitats affect local abundance and how permeable habitat boundaries are to movement of individuals. Schlosser (1991, 1995) recognized the interaction between fish movement and each of these elements. For example, a basin with high habitat complementarity could support fish populations with low movement rates and no evident population sources or sinks, whereas a basin with suitable spawning gravels in only one segment or stream and little complexity has low habitat complementarity that forces fish to migrate to reproduce and has a strong source-sink structure. Schlosser and Angermeier (1995; also see Schlosser 1998, Schlosser and Kallemyn 2000)

further explore these and related concepts with respect to fish populations.

How small- to large-scale patterns in habitat distribution and abundance affect populations of cutthroat trout, or most other salmonids, has not been fully explored. Nevertheless, Fausch et al. (2002) described some promising avenues for investigation, and a few studies suggest the importance of habitat complementarity and supplementarity, source-sink structure, and neighborhood effects to cutthroat trout. For example, Dunham et al. (1997, 2002b) concluded that the probability of presence of Lahontan cutthroat trout was related to the size of habitat patches and whether other waters to which they were connected also contained populations. Torgersen et al. (2004) found periodicity in the distribution of cutthroat trout at three spatial scales that were related to characteristics of the streams and basins, and Ganio et al. (2005) noted how this varied among streams. Large Bonneville cutthroat trout migrated from spawning sites in small tributaries and the presumably warmer and more productive feeding grounds where they overwintered (Colyer et al. 2005). Young and Guenther-Gloss (2004) found that longitudinal patterns in abundance of adult greenback cutthroat trout differed from those of juveniles in headwater streams, and that neither displayed consistent downstream-upstream trends. Putative nursery areas for Colorado River cutthroat trout (Bozek and Rahel 1991b) were not related to the abundance or distribution of suitable rearing habitat; instead, they were associated with reaches containing spawning gravels. Finally, Young et al. (2005) observed that the square root of abundance of Colorado River cutthroat trout and greenback cutthroat trout increased in proportion to stream length, and that this variable accounted for about 80 percent of the variation in abundance. They also showed that measures of individual habitat components were not strongly related to abundance, and concluded that larger streams may support disproportionately large populations because they provide a greater diversity of habitats (or higher complementarity) than do smaller streams. There is also a rapidly growing literature on predicting fish species occurrence or abundance based on landscape-scale habitat patterns (e.g., Angermeier et al. 2002, Olden and Jackson 2002, Feist et al. 2003, Peterson and Dunham 2003) that is likely to prove useful in understanding the relation between habitat abundance and distribution and cutthroat trout population size.

The importance of riparian zone structure to fish populations is also beginning to be acknowledged. Schlosser (1991) pointed out the importance of nutrient

exchange between riparian zones and stream channels, highlighting the terrestrial contributions of leaf matter to secondary productivity in streams. More recently, the two-way trophic linkages between streams and their riparian zones have been recognized (Baxter et al. 2005), and the effects of riparian vegetation composition and disturbance on fish community composition are being explored. Little has been done with inland cutthroat trout in this regard, but there can be strong effects of riparian zone vegetation and structure on aquatic macroinvertebrate production, terrestrial macroinvertebrate infall, and fish abundance (Molles 1982, Snyder et al. 2002, Allan et al. 2003, Kawaguchi et al. 2003, Perry et al. 2003). The apparent response of cutthroat trout to small-scale changes in primary productivity and light associated with forest openings (Wilzbach 1985, Wilzbach et al. 2005) and the variation in diet correlated with different riparian vegetation types (Romero et al. 2005) imply that riparian zone structure may account for some of the spatial variation in cutthroat trout abundance.

An additional perspective that is key to understanding the size and distribution of cutthroat trout populations is that habitats are dynamic and respond to processes recurring at daily, seasonal, annual, and multi-decadal intervals. In particular, disturbances that dramatically alter channels or riparian zones (e.g., debris torrents, landslides, extreme floods, and severe fires) will change the discharge-sediment transport regime, re-set forest succession and large wood dynamics, and redistribute suitable and unsuitable habitat in a basin, sometimes for decades or centuries (Reeves et al. 1995, Benda et al. 1998). These rare events, and the locations of refugia from them, can dictate the size, structure, distribution, and persistence of fish populations (Schlosser and Angermeier 1995, Labbe and Fausch 2000).

Diet

Cutthroat trout are sight-feeding predators that consume zooplankton, aquatic and terrestrial macroinvertebrates, and occasionally fish or other small vertebrates. Because maximum prey size in salmonids is constrained by gape width, fry may consume very small prey that are not bioenergetically worthwhile to larger fish (Bozek et al. 1994). Nevertheless, the small average size of most invertebrates results in substantial overlap in the sizes of items consumed by juvenile and older age classes. The high taxonomic overlap between prey and drifting macroinvertebrates indicates that cutthroat trout are opportunistic foragers (Young et al. 1997a, McGrath 2004). Nevertheless, they also exhibit

a certain degree of prey selectivity, particularly for terrestrial macroinvertebrates during summer (Young et al. 1997a, Hilderbrand and Kershner 2004), which can constitute a third to a half of the annual energy intake of salmonids in small streams (Allan et al. 2003, Baxter et al. 2005, Romero et al. 2005). There is little incidence of piscivory among populations of fish with resident life histories in small streams (Bozek et al. 1994, Dunham et al. 2000, Hilderbrand and Kershner 2004, McGrath 2004). Keeley and Grant (2001) attributed this to the general absence of forage fish and suggested that the growth of trout would decline or cease once they reached 15 to 20 cm, which is reasonably concordant with observations of cutthroat trout found in such environments (Downs et al. 1997, Hilderbrand and Kershner 2004, Young and Guenther-Gloss 2004). Piscivory may be more typical of cutthroat trout in or originating from larger streams, rivers, and lakes. For example, predation by large Bonneville cutthroat trout in Strawberry Reservoir, Utah, reduced overwinter survival of stocked cutthroat trout fingerlings to 1 percent (Baldwin et al. 2000). Also, Snyder and Tanner (1960) reported that adult Colorado River cutthroat trout still present in spawning streams contained an average of 61 fry during the late summer outmigration of juvenile fish to Trappers Lake (cf. Benson 1960).

Behnke (1992) argued that adult habitat was most often limiting in fluvial trout populations, yet the substantial influence of food availability on trout growth, density, and behavior has long been recognized (Chapman 1966). In small exclosures within streams, the addition of food markedly increased growth of age-1 cutthroat trout relative to fish not receiving supplemental food, whereas additions of cover had no effect (Boss and Richardson 2002; also see Wilzbach 1985). Direct or indirect additions of food had similar effects on other small-stream salmonids (e.g., Warren et al. 1964, Mason 1976), and with the plethora of recent papers on links between stream productivity and allochthonous inputs, such as salmon carcasses (Wipfli et al. 2004) or particular forms of riparian vegetation (Baxter et al. 2005), there is substantial evidence that food availability is dynamic at decadal and successional scales and has a large role in structuring cutthroat trout populations (Dunham and Vinyard 1997, Railsback and Harvey 2002, Young and Guenther-Gloss 2004).

Spawning

With few exceptions (Carl and Stelfox 1989), cutthroat trout spawn in lotic environments. Although they generally choose small, perennial streams (Clancy 1988, Magee et al. 1996), they sometimes

use springbrooks in the river floodplain (Joyce and Hubert 2004), alluvial side channels of main-stem rivers (Henderson et al. 2000, De Rito 2004), or even intermittent channels that remain flowing until fry have emerged (Gresswell et al. 1997). Spawning may begin as early as April and conclude as late as July in response to elevational gradients in flow and temperature (Benson 1960, Snyder and Tanner 1960, Quinlan 1980, Brown and Mackay 1995a, Schmetterling 2001, Zurstadt and Stephan 2004). This species tends to spawn during or after snowmelt-driven peaks in discharge (Quinlan 1980, Jespersen 1981, Thurow and King 1994, Schmetterling 2000, 2001, De Rito 2004), which probably evolved as a mechanism to avoid egg and fry incubation during channel-scouring flows. With regard to temperature, Thurow and King (1994) and Magee et al. (1996) observed that spawning began after mean daily temperatures exceeded 7 to 10 °C, but Quinlan (1980) found that spawning in high-elevation tributaries in southern Wyoming began when maximum daily temperatures reached these levels.

The length of incubation and time to fry emergence also vary with temperature. Snyder and Tanner (1960) reported that Colorado River cutthroat trout eggs hatched after 30 days at 10 °C, with each 0.6 °C decline corresponding to a 2-day increase in this period. Similarly, Yellowstone cutthroat trout eggs hatched 25 to 49 days after deposition when the sum of mean daily temperatures reached 278 to 365 °C (Gresswell et al. 1994). Time to emergence after spawning was 570 to 600 degree-days for Colorado River cutthroat trout (Coleman and Fausch 2007a). Because Colorado River cutthroat trout in many high-elevation streams do not appear to conclude spawning until early July, fry emergence is often in late August through early October (Young 1995, Coleman and Fausch 2007b).

Cutthroat trout are assumed to home to natal streams for reproduction, as do most anadromous salmonids (Quinn 2005a), but there is little information on this. Gresswell et al. (1994) reported that less than 5 percent of migrating Yellowstone cutthroat trout that ascended Yellowstone Lake tributaries to spawn had strayed. Schmetterling (2001) noted that westslope cutthroat trout that spawned in consecutive years used the same tributary in each year, but not the same location. Why salmonids stray or home has received less attention, but the preponderance of evidence implies that the selective advantage of local adaptation disproportionately favors homing, whereas temporal variation in habitat quality, such as from floods or drought, appears to be related to straying (Hendry et al. 2004).

The characteristics of sites chosen for spawning, known as redds, have been the focus of many studies. Females deposit eggs from 10 to 25 cm deep in spawning gravels (Snyder and Tanner 1960, Young et al. 1989), and burial depths are related to female size (Crisp and Carling 1989). Substrates chosen for egg deposition contain particles ranging from much less than 1 mm up to 100 mm, with a median diameter frequently between 10 and 30 mm (Thurow and King 1994, Schmetterling 2000). Kondolf and Wolman (1993) concluded that females could use substrates with median particle sizes of about 10 percent of fish length, although sizes actually used were constrained by what was available. Substrate composition, particularly the proportion of fine particles, has been shown to be related to the survival from egg deposition to fry emergence (Chapman 1988). Young et al. (1991) confirmed this in laboratory studies of Colorado River cutthroat trout, but they also demonstrated that measures of the central tendency of substrate composition accounted for a greater proportion of the variation in survival to emergence than did measures of fine sediment alone. Other common characteristics of redds include water velocities of 0.4 to 0.6 m per s and depths of 10 to 20 cm (Thurow and King 1994, Schmetterling 2000).

Locations with suitable velocity, depth, and substrate for spawning can be found in channels of many different configurations and created by a variety of channel features and lithologies (Bozek and Rahel 1991b, Kondolf and Wolman 1993, Magee et al. 1996). Kondolf et al. (1991) observed that in reaches with gradients averaging 7 to 17 percent, salmonid spawning areas were in sites near obstructions such as boulders or log jams that reduced local gradients to 0.4 to 3.6 percent. Many Colorado River cutthroat trout redds in small streams are associated with the shallow tails of pools where channel shape favors downwelling and deposition of appropriate-sized substrate (M.K. Young, personal observation). Although Magee et al. (1996) could not relate reach-scale variables to spawning gravel availability, Buffington et al. (2004) noted that channel roughness was related to the availability of spawning gravels, with steeper channels requiring bar formation or obstructions such as large wood to promote gravel storage.

Demography

Life history characteristics

A life history is defined as the repertoire of actions an animal performs to complete its life cycle

and enhance its fitness (Stearns 1992), and can include any phenotypic or behavioral variation that contributes to demographic and evolutionary success. Some of these characteristics have been previously discussed (see Activity patterns and movements, above) and can influence the viability of populations. The following discussion focuses on those aspects most directly related to population demography. Salmonids in general (Willson 1997) and cutthroat trout in particular (Gresswell et al. 1994, Waples et al. 2001) exhibit some of the most striking life history variation among fishes. Unfortunately, studies of this variation do not exist for many populations of cutthroat trout, and they are essentially absent from the literature on subspecies from the central and southern Rocky Mountains. Consequently, most inferences are based on data from other taxa, and must be interpreted with care.

Within a particular population, sexual maturity of cutthroat trout is more closely related to length than to age. Several studies have indicated that males will mature at shorter lengths and younger ages than will females (McIntyre and Rieman 1995, Meyer et al. 2003). Downs et al. (1997) determined that for westslope cutthroat trout in headwater streams, 50 percent of males had reached maturity at 135 mm fork length (range, 110-160 mm) and 50 percent of females were mature at 157 mm fork length (range, 150-180 mm). Males began maturing at age 2, and all were mature by age 4. Females, on the other hand, began maturing at age 3, but not all were mature until age 6. Similarly, Quinlan (1980) reported that on average, Colorado River cutthroat trout from a cold southern Wyoming stream reached maturity at 146 mm total length. The age at which cutthroat trout will reach maturity is largely determined by the productivity and temperature of a stream. For example, the mean length of age-1 fish (56 mm) in a high-elevation stream was much less than that of the mean lengths of age-1 fish (77 and 128 mm) in two mid-elevation streams in Colorado (Peterson et al. 2004a). Finally, the maximum age of cutthroat trout varies. The oldest fish observed by Downs et al. (1997) was age 8, but at least one fluvial individual in a largely unexploited population reached age 11, and 7 percent of marked fish were at least age 7 (Fraley and Shepard 2005).

The fecundity of female salmonids is related to their length, which usually accounts for about half of the variation in egg number (e.g., Downs et al. 1997). Because the majority of Colorado River cutthroat trout populations are found in small, high-elevation streams with short growing seasons, fish larger than 250 mm are often rare (Jespersen 1981, Scarnecchia and

Bergersen 1986, Young et al. 2005), and egg numbers are relatively low. In a small sample of Colorado River cutthroat trout, Quinlan (1980) reported that fecundity ranged from 95 to 281 eggs for females from 149 to 210 mm in a high-elevation Wyoming watershed. In comparable environments, westslope cutthroat trout females between 150 and 175 mm fork length produced between 166 and 264 eggs, those from 175 to 199 mm produced 198 to 553 eggs, and those from 200 to about 250 mm produced 224 to 664 eggs (Downs et al. 1997). Cutthroat trout with fluvial or adfluvial life histories typically attain greater sizes and produce more eggs (Gresswell 1995, McIntyre and Rieman 1995, Meyer et al. 2003). For example, female Colorado River cutthroat trout from Trappers Lake, Colorado, averaged 290 mm and contained a mean of 667 eggs (Snyder and Tanner 1960). These length-fecundity relations should be regarded as representative rather than predictive because they are often species- and site-specific (Gresswell et al. 1994, Downs et al. 1997).

Spawning is bioenergetically demanding, and energy consumption and weight loss by spawning trout are often high. Males expend much of this energy during competition with other males for access to females; females invest it in egg production; and mobile forms of both sexes engage in energetically costly spawning migrations (Jonsson et al. 1991). Consequently, post-spawning mortality of cutthroat trout can be high (13 to 89 percent; Gresswell et al. 1994, 1997; Vinyard and Winzeler 2000; Schmetterling 2001). Furthermore, because food availability and the growing season are often limited in headwater populations, female cutthroat trout there may only be able to accumulate enough energy to spawn in alternate years. Willson (1997) suggested that this was a typical pattern for female salmonids, but there is substantial variability among different populations of cutthroat trout. Schmetterling (2001) noted that less than half of a group of radio-tagged fluvial westslope cutthroat trout spawned in consecutive years (also see Shepard et al. 1984, De Rito 2004). Similarly, Snyder and Tanner (1960) estimated that about 16 percent of Colorado River cutthroat trout in Trappers Lake spawned in consecutive years, but they could not account for fish that strayed to other streams or died in the interim. In contrast, the frequency of spawning varied by tributary and year for Yellowstone cutthroat trout from Yellowstone Lake (Gresswell et al. 1994).

Sex ratios of mature fish have been variously estimated as favoring females or males, but this probably reflects the life history being sampled and the sampling approach. Surveys of fish during migratory

runs (e.g., at weirs near stream mouths) often suggest that females outnumber males (Snyder and Tanner 1960, Gresswell et al. 1994) while surveys of fish on spawning grounds imply the reverse (Downs et al. 1997). This pattern might prevail because the tradeoffs between increased fecundity, bioenergetic costs, and predation risk are more favorable for migratory females. Males can mature at small sizes and adopt alternative mating tactics that might be as successful as those of large males that defend females (Jonsson et al. 2001). That males can mature at smaller sizes even in resident populations implies that the adult sex ratio in general may be male-biased.

Population structure: survival rates and temporal patterns

Spatial variation among size classes or density related to habitat within a stream was discussed earlier (see Spatial patterns and temporal dynamics, above). In addition, the among-stream variation in survival rates and age structures is high and appears to be environmentally mediated. For example, annual survival rates of adult Colorado River cutthroat trout in high-elevation streams (0.53-0.57) were substantially greater than those of adults in mid-elevation Colorado streams (0.35-0.37) (Peterson et al. 2004a). These populations also differed with respect to the presence of younger age classes, which were absent in the high-elevation systems. Greenback cutthroat trout populations exhibited similar variation in size structure and probably survival because the coldest streams tended to have populations with relatively few individuals in the youngest age classes and the largest proportion of adult fish exceeding 200 mm, whereas warmer streams often contained populations with higher densities, a large proportion of the population consisting of younger individuals, and relatively few large adults (Young and Guenther-Gloss 2004). These results imply that in colder, higher-elevation systems, populations may be sustained by occasional reproductive bonanzas and the stockpiling of slow-growing but long-lived adults (cf. Kennedy et al. 2003), whereas in warmer, lower-elevation streams, year class failure may be relatively rare, density dependence among cohorts may be strong, and adult survival may be reduced (cf. Lobón-Cerviá 2005).

A number of studies have demonstrated that fluctuations in the size of salmonid populations can sometimes be extraordinary (Platts and Nelson 1988, House 1995), but sampling a limited number of reaches of individual streams at different times during different years probably exaggerated this pattern (Decker and

Erman 1992). Nonetheless, assessments partitioning the spatiotemporal variance in salmonid population size have found the temporal component to be substantial (Wiley et al. 1997, Dunham et al. 2002b, M.K. Young, unpublished data) and sometimes to be more important than spatial factors (Isaak and Thurow 2006). The spatial extent of synchrony in such fluctuations has not been comprehensively evaluated, but Young (unpublished data) found a strong positive correlation in the changes in abundance of Colorado River cutthroat trout among 14 stream segments in the North Fork Little Snake River basin over four years. Other evaluations of salmonids have detected synchrony among populations up to 30 to 50 km apart (Rieman and McIntyre 1996, Myers et al. 1997, Lobón-Cerviá 2004), but the geographic extent of events affecting fish survival will dictate this scale. For example, a severe fire would depress at most a few adjacent populations, whereas effects of climate-driven changes could extend across river basins or the entire historical range. Finally, the degree of synchrony may be related to the status of populations. Isaak et al. (2003) found that synchrony among individual Chinook salmon (*Oncorhynchus tshawytscha*) populations increased as these populations underwent a regional decline, heightening the risk of simultaneous extirpation of many populations.

Population models

Population viability models are often developed to identify those life history parameters (or vital rates) that have the greatest influence on population growth and persistence, and to simulate how variation in those parameters changes model predictions of the deterministic population growth rate or the distribution of times to extinction. There is a lively discussion in the literature on the value of such models. Their detractors contend that population viability models are rarely validated, require hopelessly large amounts of data to correctly parameterize, and produce results that are too biased, imprecise, or simplistic to generate useful predictions (Ludwig 1999, Coulson et al. 2001, Ellner et al. 2002, Lindenmeyer et al. 2003). Those defending their use often concede these points to some degree (Brook et al. 2002), but they also note that developing a population viability model compels the user to specifically describe the life history of the species of concern, to acknowledge assumptions about that life history, and to recognize critical gaps in knowledge (Morris and Doak 2004). This process also represents a reasonably objective method for making predictions about management effects and population persistence, and some model predictions have proven accurate (Brook et al. 2000). Consequently, there is

either grudging or enthusiastic support that population viability models have heuristic value because they demonstrate trends in population persistence or the response of demographic parameters to management alternatives or stochastic variation, and they have been widely adopted in the conservation field (Beissinger and McCullough 2002, Morris and Doak 2004).

Development of population viability models for conservation of cutthroat trout is limited. Hilderbrand (2003) created a projection matrix model for generic headwater stream populations of cutthroat trout (see Stapp and Hayward 2002 for a model representing an adfluvial population). Estimates of vital rates were derived from studies of Colorado River cutthroat trout (Peterson et al. 2004a), westslope cutthroat trout (Shepard et al. 1997), and the opinions of experts familiar with Colorado River and Bonneville cutthroat trout (**Table 1**). Fecundities, egg survival to fry emergence, and fry survival to the following summer were condensed into a single parameter that differed by female size. Estimates thereafter were length-based rather than age-based to reflect the influence of length on maturity, and it was assumed that half of the surviving individuals would transition to a later stage and half would remain within a particular stage. The population growth rate (λ) for this model was 1.06.

Hilderbrand (2003) explored variation in model outcomes by subjecting vital rates to deterministic and stochastic variation and constraining population growth with a density-dependence function and one of several levels of carrying capacity, as well as by mimicking the influence of different levels of immigration and population synchrony, in simulations of the probability of population persistence for 100 years. Unsurprisingly,

deterministic reductions in vital rates that reduced the population growth rate below 1.0 resulted in extinction over that interval, and larger population sizes (as measured by carrying capacity) were necessary to ameliorate the tendency of greater stochastic variation to reduce the probability of persistence. Increasing rates of immigration disproportionately improved the probability of persistence of the smallest populations, as would be expected for marginal populations dependent on larger ones for their reproductive largesse. However, synchrony in population size reduced the positive effect of immigration because when populations were large, the need for and space available to immigrants was reduced, and when populations declined, the number of available immigrants declined.

A few additional caveats about the generality of these results are warranted. Because of the diversity of life history strategies exhibited by cutthroat trout (Rieman and Dunham 2000) and the uncertainty about and inherent variability in parameter values, population viability models are most useful for indicating relative effects of changes in vital rates, rather than for demonstrating specific outcomes (Beissinger and Westphal 1998). The relative importance of vital rates also relies on the underlying model assumptions about regulating processes and population structure. For example, Hilderbrand (2003) reported that changes in survival from the subadult to small adult stage and the young-of-the-year to subadult stage had the greatest influence on population growth rate in the matrix model for cutthroat trout. In contrast, a comparable model for white-spotted charr (*Salvelinus leucomaenis*) in Japan that assumed similar fecundities, lengths, and ages but slightly different growth rates and a different form of density dependence identified adult survival rate as

Table 1. Parameter values for the components of the matrix population model developed by Hilderbrand (2003), and ranges of values for those parameters from Downs et al. (1997), Vinyard and Winzeler (2000), Stapp and Hayward (2002), and Peterson et al. (2004a)

Parameter	Value	Range
Fecundity (150-200 mm female)	139	166-553
Fecundity (200+ mm female)	231	224-664
Survival to emergence of fry	0.40	0.06
Fry overwinter survival	0.27	0.37
Age-0 to subadult survival	0.22	0.02-0.37
Subadult to subadult survival	0.16	0.23-0.42
Subadult to small adult survival	0.16	0.23-0.42
Small adult to small adult survival	0.23	0.35-0.57
Small adult to large adult survival	0.23	0.35-0.57
Large adult to large adult survival	0.23	0.11-0.57

having the greatest effect on population growth rate (Morita and Yokota 2002). Furthermore, elasticities (i.e., the values for judging the relative influence of vital rates) are only accurate for small changes in those parameters (e.g., perhaps much less than 20 percent) (Mills et al. 1999). Greater variation, particularly in the relative importance of different vital rates in different habitats, can markedly alter the elasticity rankings of vital rates among models (Mills and Lindbergh 2002, Morris and Doak 2004, Norris 2004). As was noted earlier, habitat-specific variation in vital rates for headwater populations of cutthroat trout is common. In addition, an assumption in the aforementioned cutthroat trout model (and others; Fefferman and Reed 2006) is that age structures will remain fairly constant in any given stream, but this may not be realistic. For example, Hesthagen et al. (2004) observed substantial annual variation in the mean age of maturity in female Arctic charr (*S. alpinus*) and brown trout over a 13-year interval. In addition, the repeated evolution of migratory strains suggests that fecundity may play a large role in the success of populations, at least in evolutionary time (Willson 1997), despite its relative unimportance in the previously noted demographic models. Consequently, the use of demographic models to gauge population growth and persistence can be informative, but the results must be treated with caution in the absence of long-term data (at least 4 years; Morris and Doak 2004) specific to the life history characteristics and habitat being modeled.

Genetic structure

The genetic structure of cutthroat trout populations reflects their evolutionary history and may dictate their evolutionary future. The relatively high levels of genetic variation within the family Salmonidae are thought to have arisen from an autopolyploidization event (Allendorf and Thorgaard 1984). The extraordinary phenotypic diversity of salmonids, particularly in their life histories (Willson 1997), may be linked, in part, to this genetic variation as well as to the diversity of environments they occupy (Waples et al. 2001). In cutthroat trout, there is often substantial genetic differentiation among local populations. Population genetic structure often displays a geographic cline in many salmonids (i.e., network distance sometimes explains relatedness of populations and much of the diversity is partitioned among major river basins), yet a more common pattern among cutthroat trout is to exhibit high interpopulation genomic diversity unrelated to geographic distance (Allendorf and Leary 1988, Waples et al. 2001, Taylor et al. 2003, Young et al. 2004, Cegelski et al. 2006, Neville et al. 2006a; for

comparable structure in brook trout in their native range, see Castric et al. 2001). Preliminary studies of Colorado River cutthroat trout in streams draining the Uinta Range in Utah indicated that separate clades existed in streams draining the southern and northern slopes, and that differences among populations within clades accounted for much of the overall genetic variation (D. Shiozawa and P. Evans, Brigham Young University, unpublished data). Elsewhere, cutthroat trout populations linked by migratory individuals (e.g., Yellowstone cutthroat trout in the main-stem Yellowstone River and connected tributaries) often show less divergence (Allendorf and Leary 1988, Neville et al. 2006a), but have developed distinct populations even in the presence of straying, adjacent streams less than 2 km apart (Wenburger and Bentzen 2001). A further complication is that fish with different life histories (e.g., migrants and residents), may be derived from the same set of parents or constitute the same deme (Jonsson and Jonsson 1993, Yamamoto et al. 1999, Kinnison and Hendry 2004), yet also be under selection favoring one form or the other (Klemetsen et al. 2003, Adams and Huntingford 2004).

Physical isolation, at the scale of individual streams, imposes a different set of conditions on genetic structure. Isolated populations of salmonids have shown reduced genetic diversity relative to downstream populations, a pattern that has been attributed to the pronounced effect of genetic drift on small populations of salmonids (Carlsson and Nilsson 2001, Castric et al. 2001), including cutthroat trout (Taylor et al. 2003, Neville et al. 2006a). The existence of multiple barriers within a particular basin has led to fine-scale population structuring (Pritchard et al. 2007b), often with the incremental loss of genetic diversity observed among population segments found farther upstream (Wofford et al. 2005). However, these small populations, if they persist, may simultaneously be subject to strong natural selection and become locally adapted, a process that can be relatively rapid (Ford 2004, Hendry et al. 2004; also see Genetic concerns, below).

Metapopulations

Geographically distinct populations that are demographically linked by migrants are considered to constitute metapopulations. The specific metapopulation structure depends on the size and demographic contribution of each subpopulation, the frequency, direction, and extent of migration among subpopulations, and the rates of subpopulation extinction. The key, however, is that individuals can move among locations, thereby promoting persistence in the face of localized environmental catastrophes

and reducing the long-term loss of genetic variation. This connectivity appears to buffer some populations from extirpation (Dunham et al. 1997), but it need not be continual for metapopulations to form. Rather, connectivity can be ephemeral and appear at the scale of decades or centuries (Rieman and Dunham 2000, Schlosser and Kallemeyn 2000), such as might be expected during the pre- and post-glacial history of Colorado River cutthroat trout. Although salmonids are believed to form metapopulations where circumstances permit and this concept has been a rich source of theoretical predictions (Rieman and Dunham 2000), detailed descriptions of metapopulation structure in salmonids remain rare (but for studies on aspects of metapopulations, see Dunham et al. 1997, Dunham and Rieman 1999, Koizumi and Maekawa 2004, Johansen et al. 2005, Neville et al. 2006a).

Community ecology

Sympatric vertebrates

Because they are currently largely restricted to high-elevation headwater streams, Colorado River cutthroat trout are often the only native fish species present or are sympatric with at most a few other indigenous fish species. These may include mottled sculpin (*Cottus bairdi*), mountain sucker (*Catostomus platyrhynchus*), and speckled dace (*Rhinichthys osculus*). Historically, Colorado River cutthroat trout were found in warmer, larger streams and rivers, and they were at least seasonally sympatric with a much larger array of species, including mountain whitefish (*Prosopium williamsoni*), flannelmouth sucker (*C. latipinnis*), bluehead sucker (*C. discobolus*), roundtail chub (*Gila robusta*), and perhaps Colorado pikeminnow (*Ptychocheilus lucius*). The historical dynamics of these communities are a matter of speculation because of the current prevalence of nonnative species and anthropogenic disruption of large stream habitats.

The influence of competition with or predation by native fish species on Colorado River cutthroat trout has not been studied. Incidental predation by terrestrial vertebrates, such as dipper (*Cinclus mexicanus*), belted kingfishers (*Ceryle alcyon*), great blue heron (*Ardea herodias*), osprey (*Pandion haliaetus*), mink (*Mustela vison*), and otter (*Lutra canadensis*), was probably historically common. Researchers using radiotelemetry regularly find some transmitters on stream banks (e.g., Schmetterling 2001, Lindstrom 2003, De Rito 2004, M.K. Young, personal observation) and treat these as instances of predation, although they sometimes cannot

be distinguished from the scavenging of already dead fish or angler harvest. In some areas, spawning runs may have attracted large numbers of predators, comparable to the concentrations of grizzly bears (*Ursus arctos horribilis*) and other predators that until recently exploited large spawning runs of Yellowstone cutthroat trout from Yellowstone Lake (Haroldson et al. 2005). Such spawning runs probably formed a significant energy subsidy to upland and riparian environments, but the absence of these runs for about the last century has probably represented a major trophic shift for some stream ecosystems in the central Rocky Mountains.

Parasites and diseases

There is little information on the parasites and diseases of Colorado River cutthroat trout. The trematode *Gyrodactylus* has been found in at least one wild population (Jespersen 1981), and the water mold *Saprolegnia* has been detected in many others, particularly in mature individuals after the spawning season (Binns 1977, M.K. Young, personal observation). Many pathogens, such as *Aeromonas salmonicida* (the causative agent of furunculosis), *Renibacterium salmoninarum* (cause of bacterial kidney disease), *Tetracapsula bryosalmonae* (cause of proliferative kidney disease), *Flavobacterium psychrophilum* (cause of bacterial coldwater disease), and infectious hematopoietic necrosis virus are widespread in salmonids, of sometimes unknown geographic origin, and can result in high mortality rates among hatchery populations, particularly those under stress. Their prevalence in or influence on wild populations of Colorado River cutthroat trout has not been evaluated.

Envirogram

I developed an envirogram to describe the factors that directly and indirectly influence the abundance and viability of Colorado River cutthroat trout (**Figure 3**) (Andrewartha and Birch 1984). The envirogram is divided into five panels: reproduction, growth and survival, biotic hazards, abiotic hazards, and demographic and evolutionary hazards. Because our understanding of the biology of this subspecies is incomplete, these diagrams should be regarded as hypotheses about the ecological relations between different life stages, their habitats, and their communities. However, the greatest value of this framework may be to serve as a heuristic tool for managers and to challenge researchers to test these hypotheses or propose alternatives (Graves 2001).

1. Reproduction

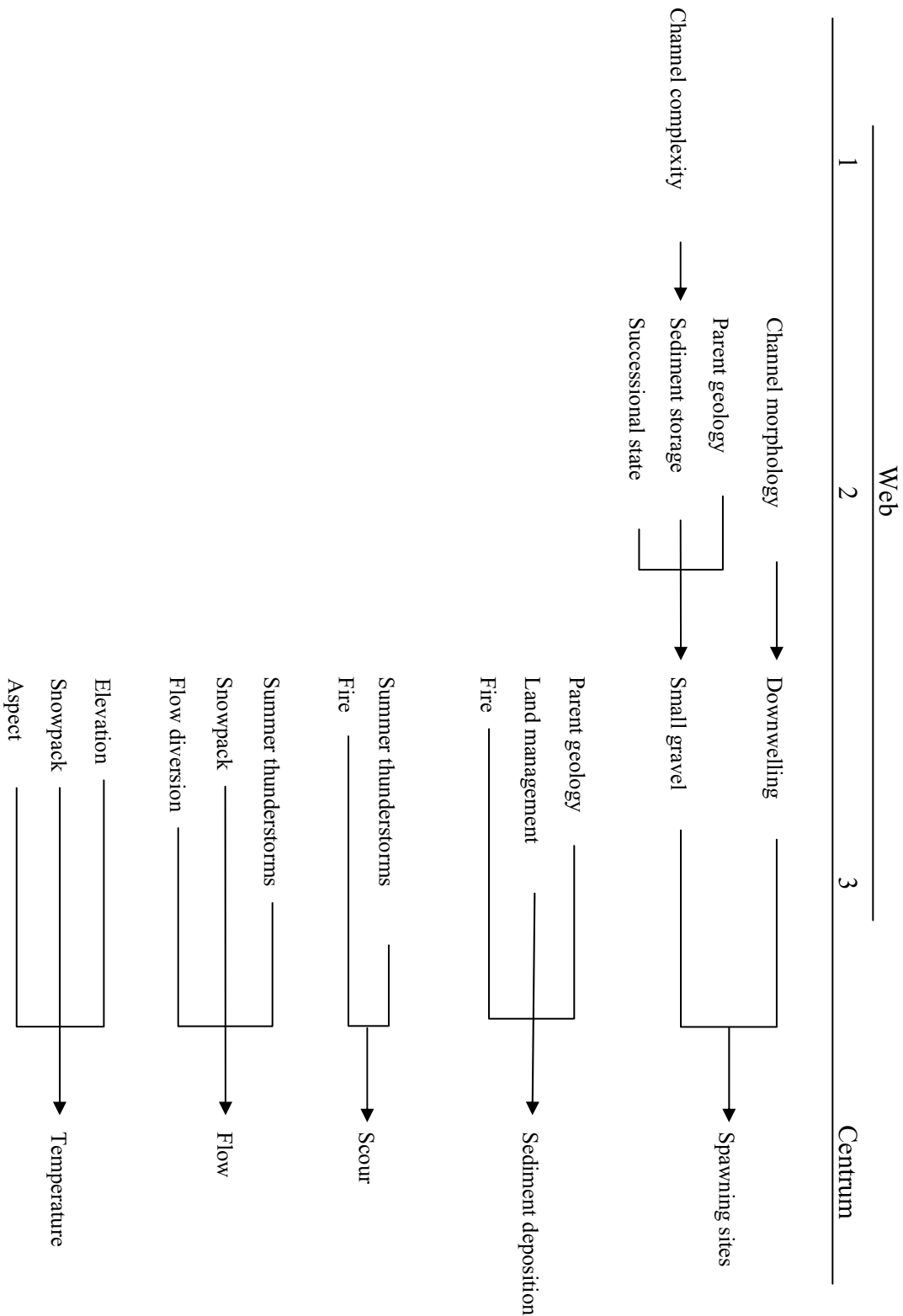
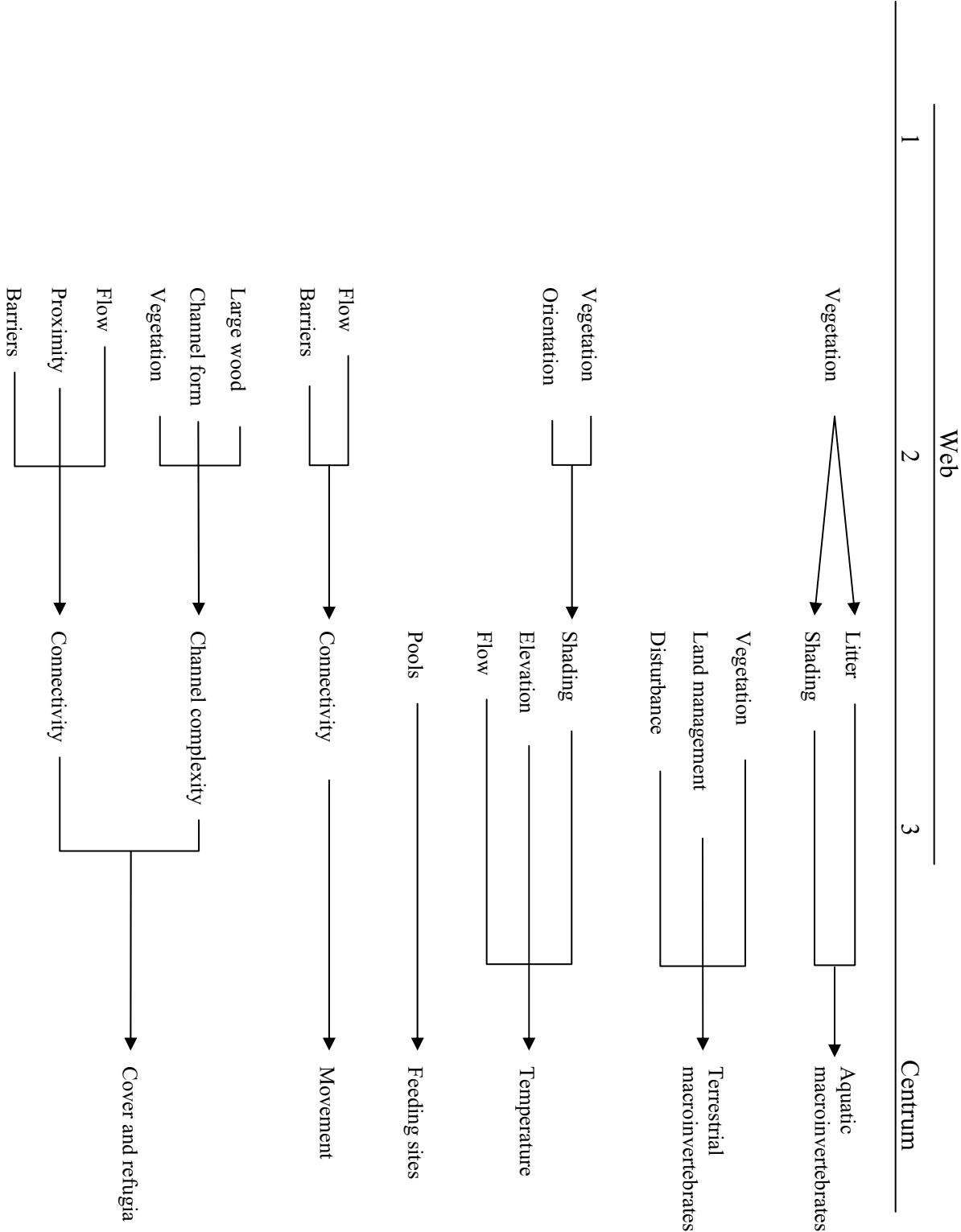
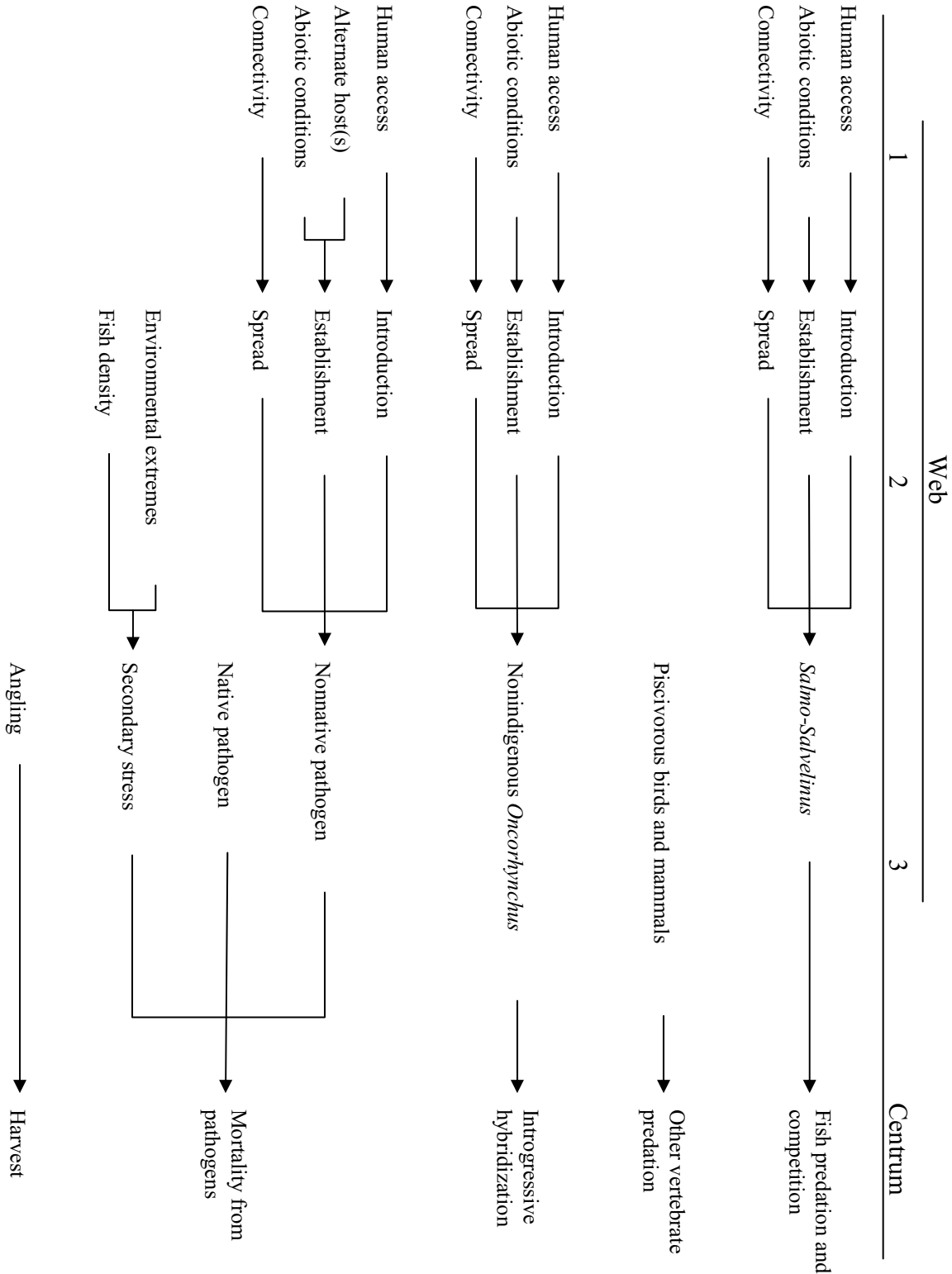


Figure 3. Envirogram of factors important to the different life stages of Colorado River cutthroat trout. Panels address **reproduction (1)**, **growth and survival (2)**, **biotic hazards (3)**, **abiotic hazards (4)**, and **demographic and evolutionary hazards (5)**.

2. Growth and survival



3. Biotic hazards



4. Abiotic hazards

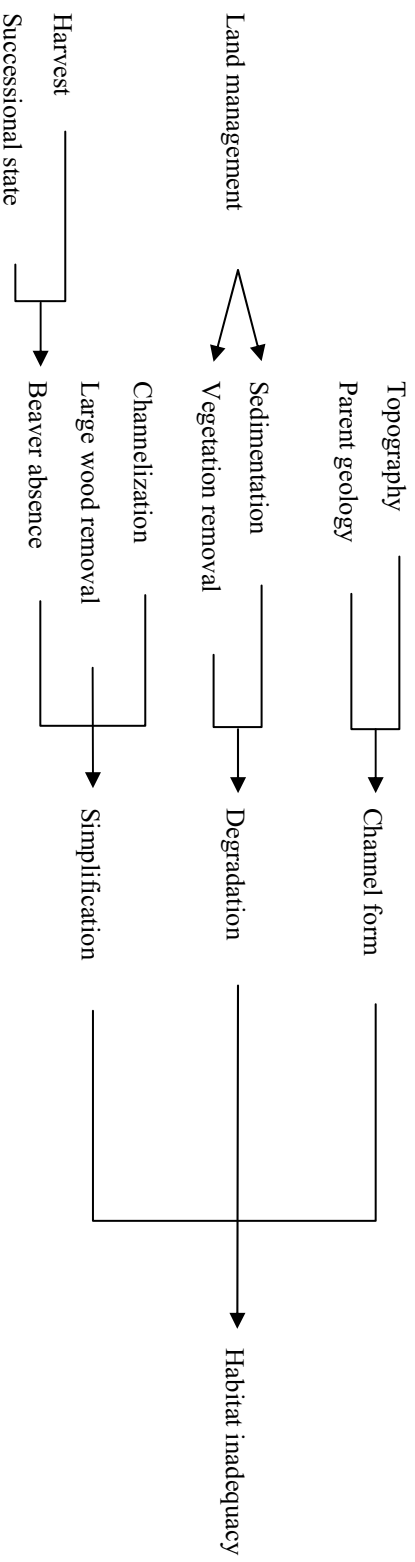
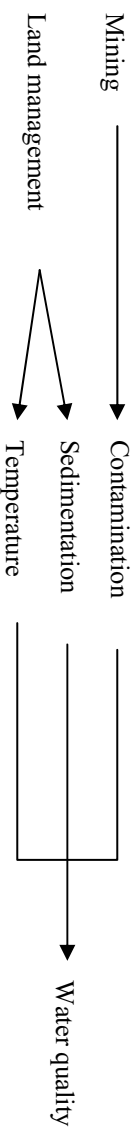
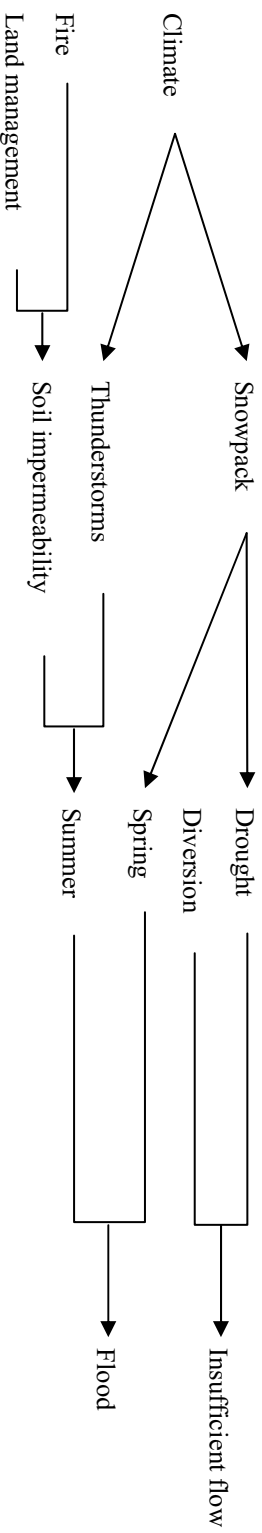
Web

1

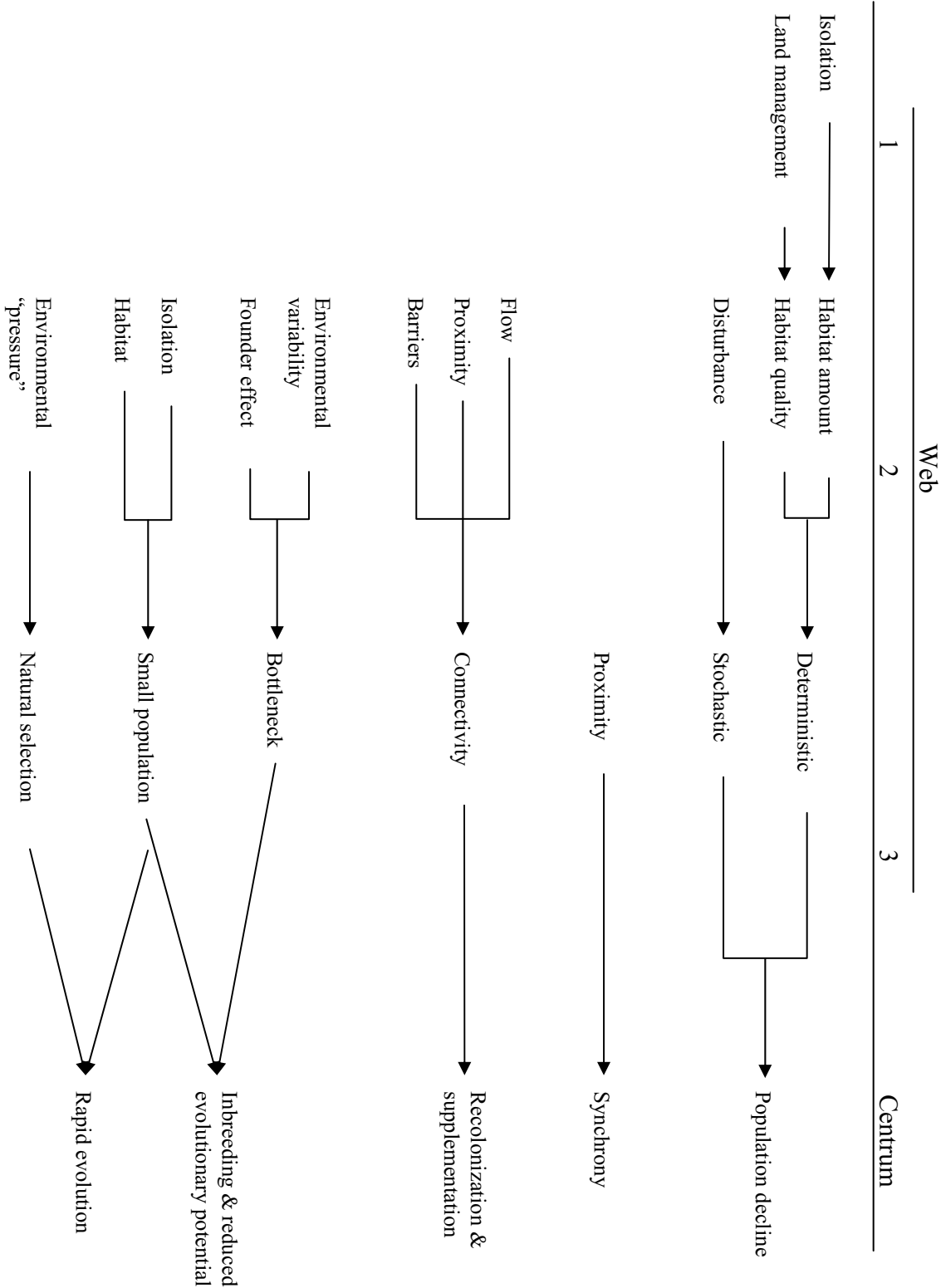
2

3

Centrum



5. Demographic and evolutionary hazards



CONSERVATION

Potential Threats

Nonnative fishes

Brook trout

Brook trout have probably been responsible for the greatest loss of headwater populations and represent the greatest immediate threat to the persistence of remaining populations of Colorado River cutthroat trout. The distribution of this nonnative species overlaps with all or part of 94 of the 285 conservation and core conservation populations of Colorado River cutthroat trout (Hirsch et al. 2006), and replacement of some populations of Colorado River cutthroat trout by brook trout is ongoing (Brauch and Hebein 2003, Peterson and Fausch 2003). This species is ubiquitous throughout the historical range of Colorado River cutthroat trout in Wyoming and Colorado, typically inhabiting the small streams that constitute the bulk of waters currently occupied by Colorado River cutthroat trout. In favorable habitats, brook trout mature at younger ages and exhibit greater size-specific fecundity than do cutthroat trout (Adams 1999, Kennedy et al. 2003), although their overall biomass may be comparable to that of the displaced cutthroat trout population (Shepard et al. 2002) or somewhat greater (McGrath and Lewis, In press).

Often, the mortality rates of young cutthroat trout exposed to brook trout are high enough to result in recruitment failure (Dunham et al. 2002a, Shepard et al. 2002, McGrath 2004, M.K. Young, unpublished data). Peterson et al. (2004a) demonstrated that age-0 Colorado River cutthroat trout survival was near zero in the presence of brook trout, and that the suppression of brook trout led to large increases in survival of age-0 and age-1 fish. However, the mechanism by which brook trout replace cutthroat trout remains an enigma. Substantial diet overlap exists between the two species (Dunham et al. 2000, Hilderbrand and Kershner 2004, McGrath 2004), and so a number of studies have focused on competition. However, these have been conducted under artificial settings, and their relevance to wild populations is uncertain. For example, in laboratory or enclosure trials, juvenile and adult brook trout occasionally dominated same-age or -size Colorado River cutthroat trout by achieving greater short-term growth rates or survival, but often only at exceptionally high water temperatures or fish densities (De Staso and Rahel 1994, Novinger 2000, Hilderbrand and Kershner 2004). Moreover, these necessarily

narrowly-focused experiments have not addressed the spatial and temporal variation in foraging exhibited by each species in circumstances other than the diurnal, mid-summer conditions emulated in the laboratory or monitored in the field. Predation by brook trout would represent a more direct explanation for the declines in age-0 and age-1 cutthroat trout, but field observations offer little support for it (Dunham et al. 2002a, McGrath 2004, B. Shepard personal communication 2007, M.K. Young, unpublished data). Nevertheless, even small brook trout have exhibited piscivory (Levin et al. 2002, Mohler et al. 2002), and there may be a particular temporal window (e.g., immediately after cutthroat trout fry emergence) when predation is substantial. As noted earlier, this period was characterized by intense cannibalism by cutthroat trout on their own fry (Benson 1960, Snyder and Tanner 1960), and the combined effects of both species may be responsible for declines in fry survival.

In most of Colorado and Wyoming, there is little evidence for substantial biotic resistance by Colorado River cutthroat trout to invasions by brook trout (cf. Benjamin et al. 2007). Even in waters with relatively robust populations of Colorado River cutthroat trout (e.g., the North Fork Little Snake River in south-central Wyoming) brook trout have been able to successfully reproduce and spread following a human-assisted introduction (M.K. Young, personal observation). Thus, a commonly observed pattern is of Colorado River cutthroat trout persisting in the extreme headwaters of a basin, with brook trout dominating all remaining suitable waters downstream (cf. Fausch 1989, M.K. Young, personal observation). Although physical barriers to upstream migration often separate these species, there are some examples of coexistence of Colorado River cutthroat trout and brook trout in the absence of barriers. It is uncertain whether these represent a transient sympatric phase (i.e., a snapshot of an ongoing invasion; Peterson et al. 2004a), a “stagnant” invasion dependent on future habitat or population disruption before proceeding further (Griffith 1988, Adams et al. 2001, Shepard 2004), or the partitioning of suitable habitats by each species. It should be noted that during a protracted invasion (i.e., over several decades) these alternatives may be indistinguishable (Spens et al. 2007). Another possibility is that life history diversity may confer an advantage to cutthroat trout found elsewhere. Yellowstone cutthroat trout in the Yellowstone River basin, westslope cutthroat trout in many rivers west of the Continental Divide in Montana and Idaho, Bonneville cutthroat trout in the Logan River, and even Colorado River cutthroat trout in larger streams draining the southern slopes of the Uinta

Range have persisted in sympatry with brook trout for decades. A shared characteristic among these basins is the existence of migratory forms of cutthroat trout that are larger and more fecund than resident forms. As noted earlier, offspring of some of these migratory fish migrate from spawning streams shortly after emergence. Because evidence indicates that juvenile cutthroat trout suffer high mortality rates in the presence of brook trout, fry migrating from waters occupied by brook trout may be achieving greater survival, thus facilitating cutthroat trout persistence. If so, the widespread fragmentation of stream networks with anthropogenic barriers (e.g., water diversions, culverts, or desiccated stream reaches; see Habitat fragmentation, below) that is probably responsible for the current absence of most migratory forms of Colorado River cutthroat trout in Wyoming and Colorado may also be compromising the ability of many populations of this subspecies to persist in the face of invasions by brook trout.

Other roles of habitat in facilitating or hindering brook trout invasions may be important. At a large scale, regional climate patterns could influence brook trout success. Fausch et al. (2001) demonstrated that the annual timing of peak flow with respect to the period of egg incubation, fry hatching, and fry emergence affected the reproductive success of rainbow trout and dictated whether invasions by this species would be successful at a global scale. An apparent difference in the invasion success of brook trout east and west of the Continental Divide in Montana may be linked to differences in winter climate (Fausch et al. 2006). At smaller scales, the distribution of habitats serving as demographic sources (e.g., warmer water or reaches in unconfined river valleys; Benjamin et al. 2007) and sinks could be controlling brook trout establishment and spread (Adams 1999, Castric et al. 2001, Petty et al. 2005). For example, despite widespread stocking, brook trout are rare in much of the upper Snake River basin in Wyoming except in a few watersheds with headwater lakes (M. Novak, Bridger-Teton National Forest, unpublished data). Although advances by brook trout have been attributed to habitat disruption (Griffith 1988), invasions of brook trout are also common in relatively pristine habitats that have not undergone recent disturbance, such as the headwaters of the Colorado River in Rocky Mountain National Park (Fausch 1989, Behnke 1992). Colorado River cutthroat trout in waters with very cold summer temperatures may suffer frequent recruitment failure (Peterson et al. 2004a, Young and Guenther-Gloss 2004), but these conditions also reduce growth rates of brook trout and increase their age at maturity (Adams 1999, Kennedy et al. 2003). It may be that Colorado River cutthroat trout adults in such conditions

have greater annual survival than adult brook trout and experience punctuated recruitment in the occasional years when low snowpack or unusually warm summer temperatures facilitate post-emergence growth of fry and their subsequent overwinter survival. Under these circumstances, cutthroat trout may resist invasions by brook trout because such waters can represent a demographic sink for brook trout (Adams 1999); however, the presence of a demographic source in warmer waters downstream could promote the repeated upstream movements of brook trout that would interact with cutthroat trout in the headwaters (Peterson and Fausch 2003). Alternatively, the conditions supporting recruitment in brook trout and Colorado River cutthroat trout may be unlikely to occur simultaneously, favoring one species or the other in different years and promoting their coexistence (cf. Seegrist and Gard 1972).

Brown trout

Although brown trout are implicated in the loss of many populations of Rio Grande cutthroat trout (Calamusso and Rinne 2004, Paroz 2005), instances where they may have replaced Colorado River cutthroat trout are less apparent. This is partly attributable to the current low overlap between species; Hirsch et al. (2006) reported that brown trout were sympatric with conservation or core conservation populations of Colorado River cutthroat trout in only 12 waters. Nevertheless, brown trout have been shown to be competitively superior to cutthroat trout in laboratory trials (Wang and White 1994) and field exclosures (McHugh and Budy 2005), and there is evidence that brown trout displace wild cutthroat trout. For example, de la Hoz Franco and Budy (2005) believed that the presence of brown trout truncated the downstream distribution of Bonneville cutthroat trout in the Logan River, and McHugh and Budy (2006) observed an array of subtle but significant changes in the growth and behavior of cutthroat trout in the presence of brown trout. Yet the relative distribution of these two species in this system has apparently been stable for decades (cf. Bernard and Israelsen 1982), and Bonneville cutthroat trout in the Smiths Fork and Thomas Fork Bear River in Wyoming and Yellowstone cutthroat trout in the Yellowstone River basin have persisted in long-term sympatry with brown trout. An important element that may be facilitating coexistence is that brown trout tend to be found in larger streams at lower elevations and do not occupy many tributaries used by cutthroat trout for spawning, which might restrict any deleterious interactions between brown trout and juvenile cutthroat trout. This downstream-upstream partitioning of stream habitats by brown trout and other salmonids (Weigel

and Sorensen 2001) and their absence from small, high-elevation streams in the central Rocky Mountains (Bozek and Hubert 1992, Rahel and Nibbelink 1999) are thought to be related to their poor recruitment at low water temperatures (Jensen and Johnsen 1999, Lobón-Cerviá and Mortensen 2005, McHugh and Budy 2005). Because brown trout eggs and fry are also vulnerable to high flows during the latter part of incubation through the early stages of emergence (Jensen and Johnson 1999, Lobón-Cerviá 2004, Lobón-Cerviá and Mortensen 2005), the timing of peak discharge in these environments may also present an obstacle to more-upstream invasions.

Rainbow trout and nonindigenous cutthroat trout

Rainbow trout and nonindigenous subspecies of cutthroat trout, particularly Yellowstone cutthroat trout (Young et al. 1996), have been widely introduced into waters originally containing Colorado River cutthroat trout. Unlike brook trout or brown trout, these congeneric taxa do not replace Colorado River cutthroat trout but instead hybridize with them (Allendorf and Leary 1988, Forbes and Allendorf 1991). Although introductions of nonnative stocks do not always result in hybridization (Weigel et al. 2003), the probability of hybridization tends to rise with the number of introductions (Bischoff 1995, Colautti 2005). These hybrids are fertile and are capable of backcrossing with genetically pure fish of either source and with other hybrids, leading to introgression of nonnative genes into the cutthroat trout population. If mating between cutthroat trout and rainbow trout or nonnative cutthroat trout is nonselective (which it may not be; see Baumsteiger et al. 2005 and Ostberg and Rodriguez 2006 for examples of assortative mating) and continues for a number of generations and if hybrids do not show reduced fitness, then the genes of nonnative stocks will pervade virtually all remaining individuals to produce a hybrid swarm within a particular area (Allendorf et al. 2001). There are many examples of the development of hybrid swarms between Colorado River cutthroat trout and rainbow trout or Yellowstone cutthroat trout (D. Shiozawa, Brigham Young University, unpublished data; R. Leary, University of Montana, unpublished data). Although laboratory studies have suggested that hybrids may suffer greater juvenile mortality (Leary et al. 1995, Allendorf et al. 2004), results from field studies have been equivocal (Allendorf et al. 2004, Rubidge and Taylor 2004, Baumsteiger et al. 2005, Rubidge and Taylor 2005).

Spatial patterns in the distribution of nonnative genes are complex. Weigel et al. (2003) reported that proximity to a source of stocked fish was only weakly related to hybridization between cutthroat trout and rainbow trout. Instead, larger streams at lower elevations were more likely to contain hybridized populations regardless of stocking location. They argued that isolating mechanisms, such as different spawning and emergence times or habitat preferences between adults of each species, were preventing hybridization from developing in headwater populations of cutthroat trout (also see Henderson et al. 2000, Ostberg and Rodriguez 2006). In contrast, Hitt et al. (2003) and Rubidge and Taylor (2005) detected the upstream progression of hybrids between rainbow trout and cutthroat trout over time, and concluded that hybrid swarms would eventually occupy most of these waters except those with migration barriers. The spread of nonnative genes appeared to rely on straying by hybrid cutthroat trout rather than pure nonnative trout (Hitt et al. 2003, Rubidge and Taylor 2004), but self-sustaining feral populations of rainbow trout in river main stems or a reservoir were also implicated (Weigel et al. 2003, Rubidge and Taylor 2005). To add further complexity, De Rito (2004) argued that introgression in resident populations of Yellowstone cutthroat trout progressed much faster than it did among fluvial populations because the latter exhibited greater temporal segregation from rainbow trout during spawning.

Once introgressive hybridization of Colorado River cutthroat trout populations has begun, options for restoring a genetically pure stock are few. Although removals of obvious hybrids have been conducted with the aim of reducing the rate of transmission of nonnative genes to future generations of salmonid populations (Busack and Gall 1981, Dowling and Childs 1992), these efforts have failed (in the absence of a thorough and sustained campaign; Campbell et al. 2002) for two reasons. First, whereas it is often possible to recognize first-generation hybrids between rainbow trout and cutthroat trout visually, backcrosses and later-generation individuals can be indistinguishable from genetically pure adults without the aid of genetic testing (Leary et al. 1996). Second, if introgressive hybridization has progressed through several generations, nearly all individuals will carry at least some introduced genes, and reducing this influence to undetectable levels is probably futile (Allendorf et al. 2001).

Conservation of these hybridized stocks is a dilemma for managers. Such populations are less

desirable because they are not genetically pure and thus are poor choices for establishing new populations or supplementing existing ones (Allendorf et al. 2001). However, because introgressed populations may contain the sole remnants of portions of the genome or display unique life history attributes, their elimination or further genetic erosion would result in the permanent loss of this evolutionary legacy (Peacock and Kirchoff 2004). Favoring one perspective over the other has introduced some inconsistencies in the management of cutthroat trout subspecies (Allendorf et al. 2004, Campton and Kaeding 2005), including their status for listing under the Endangered Species Act (Allendorf et al. 2005). Currently, those populations of Colorado River cutthroat trout exhibiting less than 1 percent introgression are prioritized for conservation and considered suitable to found broodstocks or new populations, whereas those with 1 to 10 percent introgression are deemed worthy of conservation if they display novel genetic or life history characteristics (Utah Division of Wildlife Resources 2000). However, because the level of introgression detected will vary depending on the genetic technique used (Pritchard et al. 2007a), these thresholds might better serve as guidelines rather than rigid categories.

Further complicating this issue is the likely transfer of closely related taxa, such as greenback cutthroat trout or Rio Grande cutthroat trout, into or upstream from waters historically containing Colorado River cutthroat trout and vice versa. Before 1896, greenback cutthroat trout were cultured and sometimes released on the west side of the Continental Divide; thereafter, stocking of Colorado River cutthroat trout was more common and included many waters on the east side of this divide (W. Wiltzius, Colorado Division of Wildlife, unpublished data). Using genetic procedures to determine which subspecies are represented in many extant populations is an important issue for the conservation of both species (J. Metcalf and A. Martin personal communication 2007).

Other nonnative species

The number of additional nonnative species that have been introduced into the United States is large. Despite a growing sensitivity to the consequences of these introductions, they will likely continue because of the increasing globalization of commerce and the speed and ubiquity of human-assisted dispersal (Cox 2004). Invasions of some aquatic species, such as New Zealand mudsnails (*Potamopyrgus antipodarum*), could dramatically alter aquatic ecosystems, but whether these will directly affect Colorado River cutthroat trout is unknown.

Because of the global rise in aquaculture, among the largest threats may be nonnative pathogens in cultured fish. This is believed to be the pathway followed by the myxosporean parasite *Myxobolus cerebralis*, the causative agent of whirling disease (Bergersen and Anderson 1997). This European species was detected in the United States in the 1950's and may have originated from an international shipment of frozen rainbow trout (Gilbert and Granath 2003). The subsequent distribution of infected fish resulted in its establishment in wild salmonid populations throughout the Rocky Mountain states by the 1990's. This parasite reduces survival of juvenile trout and is believed to be responsible for dramatic declines in several wild trout populations (Nehring and Walker 1996, Vincent 1996). *Myxobolus cerebralis* requires the annelid *Tubifex tubifex* as an intermediate host, and the susceptibility of salmonid populations varies with habitat suitability (generally areas with large amounts of fine sediment; Gilbert and Granath 2003), genotype of the annelid (Beauchamp et al. 2002), water temperature, the abundance of infective spores, and the age of fish exposed (Thompson et al. 1999). The extent of infection also appears to vary temporally (Downing et al. 2002); thus, the magnitude of population-level effects of an infection is unknown, but they can be expected to reduce overall survival.

Colorado River cutthroat trout are susceptible to infection and mortality from whirling disease (Thompson et al. 1999), but relatively few populations have been exposed (U.S. Fish and Wildlife Service 2004, CRCT Conservation Team 2006b). Stocking of infected fish in waters containing Colorado River cutthroat trout or the spread of infected fish from nearby waters are the most likely pathways, but other methods of spread of the parasite or its intermediate host are possible. Yellowstone cutthroat trout in tributaries to Yellowstone Lake have become positive for whirling disease despite the absence of fish stocking (of salmonids other than lake trout [*Salvelinus namaycush*]), which has led to speculation that white pelicans (*Pelecanus erythrorhynchos*) may be acting as a disease vector (T. Koel, National Park Service, unpublished data). Illegal introductions of infected salmonids by anglers may also contribute to its spread, and anglers may inadvertently transport the parasite via sediment on fishing or boating equipment. Because Colorado River cutthroat trout generally occupy cold, high-gradient streams that are unlikely to support large populations of *Tubifex tubifex*, these trout populations may have low vulnerability to infection by *Myxobolus cerebralis*. However, populations occupying streams with low-gradient segments where fine sediment is abundant (e.g., in reaches with beaver ponds, those

draining fine-grained parent material, or areas degraded by land management) may be at risk.

Genetic concerns

Inbreeding depression and loss of genetic variation

Genetic variation is the fodder for evolution of populations and species. Maintenance of genetic variation relies on a balance between natural selection, mutation, and genetic drift. Mutation rates appear to be relatively low, but both natural selection and drift can operate more rapidly. Population size plays a critical role in retention of genetic variation because heterozygosity is predicted to decline exponentially with time as a function of the effective population size, with smaller populations suffering more rapid declines than larger ones (Frankham 2005). This loss of heterozygosity is also directly proportional to the inbreeding coefficient (Allendorf and Ryman 2002). A further issue is that genetically effective population sizes can be much smaller than census population sizes. The effective population size has been demonstrated to be 10 to 20 percent of the census population size of adults for many taxa (Waples 2002, Frankham 2005). For inland salmonids, this range has been 10 to 50 percent (Palm et al. 2003, Jensen et al. 2005), with the most optimistic estimates based on the assumption that fish of several age classes reproduce in any given year (Rieman and Allendorf 2001).

Inbreeding depression is the reduction in fitness of offspring produced by breeding among relatives, and it is inevitable in small, isolated populations (Allendorf and Ryman 2002). The effects of inbreeding are thought to result from the fixation and expression of deleterious recessive alleles (Allendorf and Ryman 2002). Although it has been posited that populations that survive bottlenecks (i.e., periods of extremely low abundance) will purge these alleles, theoretical and field studies have demonstrated that purging will have at most a modest effect on inbreeding depression (Allendorf and Ryman 2002, Frankham 2005). Moreover, that a population persists after a severe bottleneck is evidence neither of successful purging nor of the absence of inbreeding depression in that population.

The consequences of inbreeding depression and the loss of genetic variation in wild populations are a point of contention. Arguments have been made that by the time populations decline to the degree that inbreeding effects would be manifest, demographic or environmental factors alone would be likely to

drive these populations to extinction (Lande 1988), or that inbreeding depression occurs but may have no effect on population viability (Caro and Laurenson 1994). Nonetheless, comprehensive assessments have confirmed that inbreeding decreases the fitness of a large array of taxa (Lacy 1997, Keller and Waller 2002, O'Grady et al. 2006), and that this effect may be more pronounced in wild populations than in captive ones (Crnokrak and Roff 1999). Although population viability models indicate that inbreeding can substantially increase extinction risk, the paucity of field studies that have reached a similar conclusion (Allendorf and Ryman 2002, Frankham 2005) creates some uncertainty about the magnitude of the effect. In addition, polyploid taxa such as salmonids may be less susceptible to inbreeding depression (O'Grady et al. 2006). Nevertheless, because the consequences of inbreeding depression (or the simple lack of genetic variation) may be most pronounced during intermittent intervals of stress (e.g., for fishes, bouts of drought, disease, or unstable or degraded habitats) when mortality may be increasing for several reasons, they may be considerable yet difficult to detect (Allendorf and Ryman 2002).

From studies of the recent isolation of salmonid populations (Neville et al. 2006a) and of populations isolated above waterfalls (Castric et al. 2001, Pettersson et al. 2001, Pritchard et al. 2007b), there is compelling evidence of declines in genetic diversity. Although some studies have failed to demonstrate a positive correlation between population size and genetic variability in salmonids (Heath et al. 2002, Laikre et al. 2002, Østergaard et al. 2003), in some of these cases straying individuals may be maintaining high levels of genetic diversity despite low effective population sizes (Consuegra et al. 2005) or numbers may have rebounded after undergoing a severe bottleneck (Pritchard et al. 2007b). In addition, there is likely to be genetic structuring within populations caused by the presence of physical barriers to upstream migration, with the upstream-most segments having the least genetic variation (Wofford et al. 2005). These apparent "within-population" barriers may be relatively common (M.K. Young, personal observation).

Unintentional selection

The artificial culture of salmonids is widely practiced in the western United States, and its development has tracked advances in the transportation and exploitation of fish stocks (Wiltzius 1985). Other than severe inbreeding, early managers of hatcheries often ignored genetic concerns associated with cultured

stocks, focusing more on growth rates, survival to harvest, and ease of culture. Concerns about the genetic health of hatchery stocks have arisen because their use to found or supplement wild populations, particularly of increasingly rare salmonid taxa (Flagg et al. 2004, Mobrand et al. 2005), may substantially erode the fitness of wild stocks (Goodman 2005). Brannon et al. (2004) pointed out that there is nothing inherently wrong with hatcheries or cultured fish, but both have often failed to live up to their potential with respect to the conservation of indigenous stocks. In that regard, a symposium (Nickum et al. 2004), journal issue (Journal of Fish Biology 65[Supplement A]), and spate of recent papers (e.g., Levin et al. 2001, Brannon et al. 2004, Mobrand et al. 2005) have addressed the many advantages, shortcomings, and strategies related to using hatchery stocks to achieve conservation goals. Although there is agreement that hatchery stocks can play a role in the genetic management of wild populations (Brannon et al. 2004, Wares et al. 2004), concerns about artificial production of salmonids remain, in part because some degree of unintentional selection of those populations, even with infusions of genes from wild fish, is inescapable (Ford 2002, Quinn 2005b, Wedekind et al. 2007; with respect to greenback cutthroat trout, A. Martin, J. Mitton, and J. Metcalf, University of Colorado, unpublished data).

A ubiquitous goal of conservation plans for cutthroat trout (e.g., U.S. Fish and Wildlife Service 1998, CRCT Conservation Team 2006b) has been the development of hatchery broodstocks for both conservation and sport fishing. Mobrand et al. (2005) noted that these goals are distinctive enough to warrant separate hatchery strategies, and fundamental to the use of hatcheries for conservation is a genetic management plan to identify how genetic variation will be maintained and artificial selection avoided in hatcheries as well as how genetic effects of introductions of hatchery fish to supplement or found wild populations will be monitored (for a partial example, see Wares et al. 2004). With respect to maintaining genetic variation and avoiding artificial selection, Campton (2004) asserted that hatcheries should strive to achieve an even sex ratio, maximize the effective population of breeders, ensure an equal opportunity to spawn, and in particular avoid the practice of mixing the milt of multiple males (also see Wedekind et al. 2007). These and many other practices have been adopted in the management plans for the two Colorado River cutthroat trout broodstocks in Wyoming (Wyoming Game and Fish Department 2007).

Although rarely considered, another example of unintended selection involves the rapid evolution of isolated populations of formerly mobile salmonids (Stockwell et al. 2003). Changes in the migratory opportunities of salmonid populations can lead to selection for different life history forms and divergence in the genetic structure, and these changes can develop in surprisingly few generations (Hendry 2004). Koskinen et al. (2002) concluded that selection was largely responsible for the divergence among isolated populations of grayling (*Thymallus thymallus*) introduced 80 to 120 years earlier, despite the potential for severe founder effects and genetic drift. Ironically, whereas a number of migratory runs of salmonids have been established far outside their historical ranges (Withler 1982), there has been little success at reestablishing native salmonid populations with mobile life histories, especially in complex environments (Withler 1982, Healey and Prince 1995, Ford 2004). In some cases, isolated salmonid populations still produce occasional migrants, but downstream conditions have been altered to the extent that migrants are no longer adapted to these environments and most fail to return (Waples et al. 2001, Nelson et al. 2002). Isolation in fairly uniform habitats also poses the additional risk that populations may specialize, speciate, and lose the plasticity necessary to persist in changing environments (Gislason et al. 1999). Finally, research on sympatric forms exhibiting resident and anadromous life histories suggests that headwater isolation of cutthroat trout may produce strong yet conflicting selection. Morinville and Rasmussen (2003) concluded that low-productivity habitats led to slow growth and fish that were likely to adopt mobile life histories. In contrast, nutrient-rich environs that enabled faster growth and early maturation were associated with greater probabilities that fish would adopt residency (Willson 1997, Klemetsen et al. 2003). Thus, it seems plausible that the abrupt isolation of populations in cold, unproductive headwaters might simultaneously select for migratory life histories in juveniles because of growth limitations, and select against migration when adults are unable to return over barriers to spawn in natal habitats. Strong selection for adapted life histories under such circumstances would be unsurprising, as would substantial alteration from the historical genotypes and phenotypes present in a drainage. Despite all of these concerns, there are examples of large numbers of migrants attempting to return to their natal waters despite over a century of isolation (see Habitat improvement, below), suggesting that this life history strategy may be strongly conserved in some populations.

Harvest and recreation

Although exploitation historically played a role in the decline and extirpation of many populations of Colorado River cutthroat trout (Wiltzius 1985), there is no evidence that angler harvest is contributing to the continued depression of populations. Restrictive angling regulations (i.e., limited or no harvest and gear restrictions) apply to many populations of this taxon (Brauch and Hebein 2003, U.S. Fish and Wildlife Service 2004), and the remote locations of and limited access to most waters with this subspecies, as well as the small asymptotic length of most adult fish in streams, undoubtedly reduces fishing mortality. It is more difficult to determine whether angling in and of itself might contribute to a decline in populations of this subspecies. Paul et al. (2003) developed a model that suggested that incidental mortality of cutthroat trout in a no-harvest fishery might be sufficient to favor brook trout, for which harvest was permissible, when both species were present. However, this result relied on model assumptions rather than on empirical observations, and it appears questionable given that Yellowstone cutthroat trout in the Yellowstone River below Yellowstone Lake were captured an average of nine times each summer without obvious declines in that population (Schill et al. 1986). Evaluation of some of the more popular fisheries for Colorado River cutthroat trout could shed light on this issue.

Other forms of human recreation generally are regarded as relatively benign with respect to cutthroat trout. Concentrated human use in riparian zones has led to habitat degradation, but these effects are localized and unlikely to threaten entire populations. More critical may be the intentional or inadvertent role of humans as vectors for non-native species. Although agency-sponsored stocking of sport fishes was the primary means of arrival of many nonnative salmonids, illegal introductions by anglers have been responsible for much of the recent spread of these fishes (Rahel 2004). Hepworth et al. (2002) noted that over the last 25 years, anglers have moved nonnative fish into most southern Utah reservoirs larger than 100 ha, including several used for cutthroat trout recovery. These introductions may also be fostering the dissemination of pathogens (Whirling Disease Initiative, Montana Water Center, unpublished data). Recent studies are using forensic techniques to identify the water or hatchery of origin of nonnative species (e.g., Munro et al. 2005), but this may do little to alter the process of introduction. Also at issue is the dissemination of nonnative species or diseases on angling gear or vehicles. Controlling the spread of nonnative species

by either means may require manipulation of the transportation system (e.g., eliminating stream fords or closing roads to render intentional redistribution of nonnative fish more difficult).

Abiotic events and processes

Habitat fragmentation

As suggested by Smith et al. (2002) for fishes of the Great Basin, the distribution of Colorado River cutthroat trout has probably been characterized by expansion into low-elevation rivers and perhaps greater connectivity during periods of glacial development and greater precipitation, interspersed with retreats into smaller, accessible, high-elevation habitats that promoted greater isolation among populations during warmer, more arid times. Further habitat fragmentation undoubtedly arose following glacial retreat as stream downcutting and isostatic rebound contributed to the formation of waterfalls and cascades that terminated upstream migrations of Colorado River cutthroat trout and isolated small populations in many streams throughout its range. However, the relatively recent exclusion of this subspecies from cool, mid-elevation rivers by nonnative trout, habitat alteration, and exploitation, and the inadvertent or intentional anthropogenic isolation of small-stream populations have resulted in population insularity perhaps without precedent in the modern evolutionary history of this taxon.

Anthropogenic habitat fragmentation has resulted from several sources: impassable transportation crossings, stream desiccation or vertical barriers associated with water diversions, thermal or chemical barriers (or long reaches of unsuitable habitat) from habitat degradation, and downstream biotic barriers consisting of a gauntlet of nonnative species. These different types of barriers are widespread (Pepin et al. 2002), and in many instances the locations of the more prominent ones are known (Hirsch et al. 2006).

The genetic consequences of population isolation, particularly of small populations, were described earlier. Demographic risks include susceptibility to environmental catastrophes that can extirpate entire populations, such as the debris torrents triggered by thunderstorms in recently burned watersheds that eliminated populations of Gila trout (Brown et al. 2001). Variability in habitat suitability from annual fluctuations in precipitation and discharge may be high in the headwater habitats currently occupied by most populations of Colorado River cutthroat trout,

and the demographic variation that results can lead to population loss even when population growth rates are greater than one (Morris and Doak 2004). Alternatively, newly isolated habitats may lack resources critical to the survival of all life stages of cutthroat trout populations, which would likely result in a deterministic decline, sometimes to extinction, of such populations. In all cases, isolation prevents the natural demographic rescue of declining populations or refounding of extirpated ones.

Several studies have provided direct or indirect evidence of the consequences of habitat size for persistence of isolated salmonid populations. Harig and Fausch (2002) noted that successful introductions of Rio Grande or greenback cutthroat trout were more likely in watersheds greater than 14.7 ha. Similarly, watershed area or stream network size was positively correlated with the probability that bull trout (*Salvelinus confluentus*; Dunham and Rieman 1999), Lahontan cutthroat trout (Dunham et al. 2002b), or Dolly Varden (*S. malma*; Koizumi and Maekawa 2004) would be present in a stream segment. Probably the best evidence of isolation effects, however, comes from studies of white-spotted charr in Japan. Morita and Yamamoto (2002) found that the time since isolation increased the risk of population extirpation and the size of the watershed above a barrier decreased this risk. These authors also forecast the loss of 12 additional populations; although these habitats were still occupied, they regarded the sites as too small to support populations indefinitely based on their model. The extended time to extinction of populations doomed to fail because deterministic growth rates were less than one (or infrequent stochastic events were inevitable) has been predicted elsewhere (Morita and Yokota 2002, Hilderbrand 2003). Such populations and their condition have been described by (Hanski et al. 1996) and contradict the notion that because cutthroat trout populations occasionally are found in very short stream segments, such habitats represent adequate habitat for cutthroat trout. Soulé (1987) termed this logic “the fallacy of the accident” because it ignores the likelihood that far greater numbers of populations in such habitats have already gone extinct.

Anthropogenic habitat degradation

Recounting the vast number and extent of activities that have reduced the quality of habitat for Colorado River cutthroat trout is not possible. Hirsch et al. (2006) noted many of these but could not assess their effects on individual populations (also see Shepard et al. 2005). The consequences of various forms of land

management for salmonid habitat quality have been the subject of a thorough review (Meehan 1991), and an excellent overview of changes in Colorado rivers and streams wrought by human activity is given by Wohl (2001; and of rivers throughout the country, Wohl 2004). The effects of the major activities will be briefly reviewed here, but the reader is encouraged to consult the extensive literature for more details (see Winters et al. 2004 for a summary).

Historical changes in habitat quality from human activity were associated with the arrival of Euro Americans in the early to mid-1800's. Trapping led to declines in the abundance and distribution of beaver (*Castor canadensis*) – and more importantly, their dams – from low-gradient stream reaches. The loss of beaver dams and ponds reduced water storage that would have otherwise sustained late summer low flows, removed winter habitat and refugia, and increased stream flashiness as channel roughness decreased (Collen and Gibson 2001). This probably reduced overall abundance of Colorado River cutthroat trout in larger systems, and led to extirpations in smaller ones where such habitats were critical. Although beaver have recovered somewhat, they are believed to have reached only 10 to 25 percent of their historical abundance (Naiman et al. 1986).

Various forms of mining led to the wholesale loss of populations in waters of all sizes. Stream-based mining, such as sluicing, hydraulic mining, or dredging, completely altered stream channels (and sometimes valleys) and created sediment loads without historical precedent. Toxicants introduced from underground sources as well as the intentional or accidental disposal of solvents used to extract metals from raw ore rendered streams uninhabitable for many forms of life. Colorado has over 7,000 abandoned mines, and mine drainage influences over 2,600 km of streams (Rueth et al. 2002). Recovery from channel alteration may require centuries, and heavy metal leaching from hardrock mines may be difficult to mitigate for the foreseeable future. Currently, mining undergoes much more stringent environmental regulation, but this has not removed the possibility of catastrophic events, as was demonstrated in the late 1980's by the sodium cyanide spill and biotic sterilization of a long reach of the Alamosa River following the heap leach pond failure at the Summitville Mine. That the 1872 Mining Law continues to hold sway suggests that future effects of mineral development on fish populations are possible. The ongoing boom in oil and gas development has been accompanied by an increase in road building that may contribute sediment to cutthroat

trout streams; it is estimated that roughly 20 percent of the historical range of Colorado River cutthroat trout may be exposed to these activities (Trout Unlimited, unpublished data). The anticipated development of oil shale reserves in Colorado and Wyoming may bring similar risks. Recreational hydraulic mining for small deposits of precious metals probably has localized effects from increased suspended sediment concentrations (Thomas 1985).

Timber harvest began in earnest coincident with the demand for mine timbers and fuel, but it reached an initial peak upon the arrival of the railroad in the late 1800's with the requirement for railroad ties (Wroten 1956). Because no road system existed, streams channels were used to transport up to tens of millions of railroad ties annually to railheads farther downstream. These tie drives were conducted during high spring flows after the winter-long harvest of timber. Streams were often ponded behind temporary dams, which were blown out to release a rush of water and wood. To prevent jams from developing, streams were often cleared of large wood and boulders with dynamite before the drives began. This has left a legacy of simplified stream channels and early successional riparian zones that probably support cutthroat trout populations at reduced densities relative to historical levels, and will continue to do so until riparian stands become large enough to contribute large wood to channels (Young et al. 1994).

Overall, logging on federal lands in the Rocky Mountains has decreased as recreational use of those areas has increased (Rueth et al. 2002). Riparian timber harvest has largely ended; thus, the likelihood of large wood contributions from riparian zones to stream channels is increasing (Fausch and Young 2004). In part, more recent timber management has had a lesser effect on stream channels simply because of a larger road network, but that network has been a chronic contributor of sediment (Eaglin and Hubert 1993, Trombulak and Frissell 2000) and the cause of fish barriers in the form of impassable culverts (see Habitat fragmentation, above) and simplified habitats from channelization of streams adjacent to roads.

Livestock grazing was also historically far more intensive than at present, but in certain areas, it still degrades habitat of streams with Colorado River cutthroat trout. Although grazing effects are often confounded with other factors and sometimes difficult to isolate (Rinne 1999), the preponderance of evidence suggests that concentrations of livestock in riparian zones often lead to bank damage, higher sediment delivery, and the removal of woody and

herbaceous vegetation (Belsky et al. 1999, Agouridis et al. 2005), all of which can contribute to trout population reductions. However, different grazing systems are likely to have different effects on stream channels. For example, relative to high-intensity, short-duration grazing by cattle, season-long grazing was associated with declines in terrestrial macroinvertebrate infall and aquatic macroinvertebrate drift and reduced trout density and biomass in Wyoming streams (Saunders and Fausch 2007). In addition, use of channels by cattle that coincides with the incubation of trout eggs and alevins may lead to redd trampling and reduced embryo survival (J. Brammer, Beaverhead-Deer Lodge National Forest, unpublished data).

The magnitude of water development within the range of Colorado River cutthroat trout is staggering. Colorado has over 67,000 points of water diversion on or within 10 km of national forests and grasslands, and statewide, diversions have legally binding water rights that are 150 times the mean historical runoff for the entire state (Pepin et al. 2002). Although the primary problem associated with water development has been habitat fragmentation, the altered timing and magnitude of flows has also contributed to a lessened capacity to support cutthroat trout populations. Diversions often reduce discharge during the late summer irrigation season, which is also the time of greatest growth in cutthroat trout; hence water removal is essentially equivalent to a reduction in the amount of habitat and thus the size a population can attain. Diversion structures can also entrain large numbers of downstream-migrating fishes that fail to escape from irrigation channels when flow is discontinued (Zydlewski and Johnson 2002, De Rito 2004). For example, greenback cutthroat trout were found trapped below a diversion structure in an irrigation ditch draining Como Creek, one of the few waters with a historical population of this subspecies (M.K. Young, personal observation). In addition, snow-making operations associated with ski areas may alter the hydrograph by shrinking autumnal flows and promoting larger and later snowmelt runoff that could depress recruitment in cutthroat trout populations. Localized cloud seeding for enhancing winter snowpack could have a similar effect on peak flows, but both practices might beneficially enhance late summer base flows.

Finally, urbanization is likely to be detrimental to Colorado River cutthroat trout populations. The Rocky Mountain states are experiencing some of the fastest growth in the country; the annual growth rate was 3 percent compared to 1 percent in the rest of the United States in the 1990's (Theobald and Hobbs 2002). In

Summit County, Colorado, the population tripled between 1975 and 2000, and Douglas County, Colorado was one of the fastest growing counties in the nation in the 1990's (Travis et al. 2002). By 2030, an additional 1.5 million people are projected to live in Colorado (U.S. Census Bureau, unpublished data; available at <http://www.census.gov/population/www/projections/projectionsagesex.html>). The primary risk of increasing population growth is the lack of a concomitant decline in per-capita resource use. This is likely to reduce management flexibility to restore cutthroat trout populations because of other demands for resources, particularly the consumptive use of water and schemes to route it to locations of greatest demand. Intensified use of public lands for a variety of purposes, greater occupation of private land adjacent to or surrounded by federal lands, and litigation associated with both appear likely to constrain opportunities to retain or restore natural disturbances that may be essential to habitat formation. This suggests that action to promote Colorado River cutthroat trout conservation may be easier now than it will be in coming decades. Finally, an indirect consequence of this growing population is air pollution. Although the most widespread effects of fossil fuel consumption by a growing population are probably being manifest in a changing climate (see below), burning of hydrocarbons in conjunction with agricultural fertilization has increased the deposition of atmospheric nitrogen in nearby mountains, which could result in localized acidification of waters draining basins that lack sufficient buffering (e.g., along the Colorado Front Range; Bowman et al. 2002).

It is difficult to address the cumulative effects of these activities for any particular population of Colorado River cutthroat trout. However, it is telling that the vast majority of relict populations in Colorado and Wyoming are found on public rather than private lands, and that they disproportionately occur in USFS wilderness areas and in national parks that are largely free from the aforementioned forms of land management (Hirsch et al. 2006). A similar pattern has been observed for many salmonids in the Rocky Mountains and Pacific Northwest (Kershner et al. 1997, Lee et al. 1997, Thurow et al. 1997, Shepard et al. 2005).

Natural disturbance

Because cutthroat trout evolved with the natural disturbance regimes of the Rocky Mountains, it is assumed that these disturbances did not represent a widespread threat to their persistence. While the currently restricted distribution of Colorado River cutthroat trout has altered the risks that natural

disturbance can pose, such disturbance may also present opportunities for enhancing or restoring populations of cutthroat trout.

Fire: The immediate and long-term effects of wildfire on aquatic ecosystems and fish populations are receiving greater attention in the literature (Young et al. 2003). Occasionally, thermal or water chemistry changes associated with severe wildfire have led to direct mortality of trout populations (Rinne 1996, Howell 2006), but many populations have endured such fires with few or no ill effects or showed only temporary declines (Rieman and Clayton 1997, Gresswell 1999, Burton 2005, Sestrich 2005). More problematic may be post-fire floods, blackwater events, and debris torrents triggered by summer thunderstorms that have reduced or eliminated salmonid populations (Bozek and Young 1994, Brown et al. 2001). Cannon (1999) observed that the probability of some form of post-fire debris flow was about one in three in portions of the Rocky Mountains, and it was largely dependent on storm events in which rainfall intensity exceeded soil infiltration capacity. Given such storms, the proportion of a tributary basin burned by high-severity fire was the best predictor of the location of a debris torrent (Hyde 2003). Nevertheless, the majority of events are in small (<2.6 km²), steep (>20 percent) basins (Parrett et al. 2003), and these would usually not threaten entire populations (Rieman and Clayton 1997, but see Brown et al. 2001). The probability of such events often declines rapidly in subsequent years (Cannon 1999).

Secondary effects of fire may depress or boost populations. Channel stability often declines following fire because of the loss of riparian vegetation, increases in stream flow produced by reductions in evapotranspiration, and increases in sediment, but regrowth and resprouting of vegetation eventually attenuate off-channel contributions of sediment and water. Infall of fire-killed snags will spike in the first few decades following fire (Lyon 1984, Bragg 2000), which may lead to extremely complex channels with an array of complementary habitats. Growth rates of salmonids in burned streams often increase dramatically (J. Dunham, U.S. Geological Survey, unpublished data). Although this may in part be attributable to temporary changes in water chemistry, it is more likely that decreased shading increases primary productivity that leads to greater macroinvertebrate abundance and food availability (Wilzbach et al. 2005). Because water temperatures are directly related to the amount of solar radiation reaching the water surface (Johnson 2004), post-fire temperatures are expected to increase. This may harm or bolster population

growth rates depending on the pre-fire temperature regime (Dunham et al. 1999, Harig and Fausch 2002, Schrank et al. 2003). Streams previously too cold for consistent reproduction may support larger, more stable populations, whereas those that are already relatively warm may become seasonally uninhabitable. Both conditions will gradually revert to their original state as canopy cover and stream shading increase.

Fish community changes have also been hypothesized following fire. For example, nonnative species might invade post-fire habitats because the increased light, water temperature, sediment transport and deposition, and channel instability typical of such sites may favor nonnative salmonids (Dunham et al. 2003b). What little evidence exists, however, does not support this position. Sestrich (2005) found that brook trout invaded one system following fire but were depressed in several others while westslope cutthroat trout tended to recover rapidly and sometimes exceeded pre-fire abundances in most streams. In another basin, all native and nonnative salmonids reestablished themselves in streams after undergoing fire-related fish kills (Howell 2006).

Fire occurrence in the central Rocky Mountains appears to be somewhat predictable. Schoennagel et al. (2005) found that large fires in subalpine forests of Rocky Mountain National Park were disproportionately associated with the coincidence of certain phases of multi-year climate cycles – the negative phase of the Pacific Decadal Oscillation and La Niña events – that promoted extreme drought in the year of the fire. In these and other high-elevation Rocky Mountain forests, antecedent conditions (e.g., weather in previous years) had little effect on fire incidence.

Other forest disturbance: Two other forest disturbances that may influence cutthroat trout populations are prevalent in the central Rocky Mountains: large-scale blowdown and stand mortality from insects. With regard to blowdowns, their highly localized nature is unlikely to affect large numbers of streams (Lindemann and Baker 2001). Those that do undergo blowdown may be heavily shaded for decades, which may reduce primary productivity and stream temperature, but will also represent a source of large wood that will contribute to habitat complexity and possibly a series of temporary barriers to fish movement.

Insect-related mortality of conifers is a growing issue throughout the Rocky Mountains (Harris 2004).

However, many of its effects are expected to be comparable to those of fire (i.e., decreased shading and pulsed deposits of large wood in stream channels; Bragg 2000) and may represent a net benefit for cutthroat trout populations, particularly in those systems from which large wood has been lost due to human activities. It is presumed that the increased abundance of large wood will increase local fire intensity and fish mortality, but the interaction between fallen trees, fire characteristics, and management is highly controversial and has not been scientifically resolved (Rieman et al. 2003, Beschta et al. 2004, Karr et al. 2004).

Floods and drought: High flows following snowmelt are believed to reduce abundance of juvenile nonnative salmonids in Rocky Mountain streams (Nehring and Anderson 1993, Latterell et al. 1998), but because cutthroat trout generally spawn after flows peak in spring, the likelihood of redd scouring is low. However, the monsoonal thunderstorms in late summer typical of southern Wyoming and Colorado (Fausch and Young 2004) coincide with the period of egg incubation and fry emergence of cutthroat trout, and eggs, alevins, and fry may be susceptible to storm flows. Occasionally, such storms are severe enough to cause localized debris flows with more pronounced effects on trout populations and habitats (Roghair et al. 2002, Sato 2006). A minor debris torrent in the headwaters of the North Fork Little Snake River associated with a late August thunderstorm in 1999 effectively eliminated Colorado River cutthroat trout from a 600-m stream reach, and densities remained low in subsequent years (M.K. Young, unpublished data). The dendrochronological age of an alluvial plug above an abandoned channel in a nearby tributary provided evidence of a somewhat larger event 40 years earlier in this basin (M.K. Young, unpublished data).

In contrast, droughts are a common, broad-scale phenomenon recurring at the interval of decades to centuries in the Rocky Mountains (Kittel et al. 2002), and drought-related declines in discharge reduce trout abundance and growth rates because of high temperatures and less available habitat (Elliott et al. 1997, Hakala and Hartman 2004, Harvey et al. 2006). Persistent drought has extirpated several populations of Colorado River cutthroat trout (Brauch and Hebein 2003), although the low flows and extended growing seasons probably promoted successful recruitment in the coldest perennial streams (Isaak and Hubert 2004). Until recently, it appeared that droughts had relatively temporary effects on Colorado River cutthroat trout, but historical climate patterns may no longer be applicable.

Climate change

Climate change is an accepted fact among climate scientists. There is unequivocal evidence that the atmosphere is warming – 0.74 °C in the last 100 years, with the last 50 years likely the warmest in the past 1300 years – and little doubt that anthropogenic activities are partly responsible (Intergovernmental Panel on Climate Change 2007). Because of the link between climate change, atmospheric carbon dioxide concentrations, and fossil fuel consumption, there is every reason to believe that warming will continue. For example, the U.S. Department of Energy (2006) forecasts that global consumption of coal will nearly double by 2030; this increase will be largely due to an increased demand in fuel for electricity, which is expected to more than double. Combustion of coal is the leading contributor to the anthropogenic production of greenhouse gases, and global carbon dioxide emissions are also expected to double in the next 25 years.

The environmental effects of climate change are being felt worldwide and in the Rocky Mountains. Snowpacks in the western United States are now melting 1 to 4 weeks earlier than they did 50 years ago, flows are peaking earlier, and late-summer baseflows are declining (Mote et al. 2005, Stewart et al. 2005). The biota are responding as well; the spring arrival of migrating birds and emergence of hibernating mammals in the Colorado Rocky Mountains have advanced several weeks over the past few decades (Inouye et al. 2000), the range of macroinvertebrate species in northern Europe has begun to retract uphill and farther north (Franco et al. 2006), and similar changes in phenology or distribution are being exhibited by disparate taxa throughout the world (Parmesan and Yohe 2003, Root et al. 2003). The effects of climate change on specific populations of Colorado River cutthroat trout are difficult to predict because of site-to-site variation in the contribution of groundwater and surface flow to discharge, the uncertain applicability of predictions from global circulation models to particular regions, and the challenges of forecasting climate in montane environments (Christensen et al. 2007). Nevertheless, the regional trends and forecasts have profound implications for the viability of this subspecies. The consensus from climate model predictions is that high-latitude and high-elevation sites will receive greater winter precipitation but that more will fall as rain and the snowline will rise (Kittel et al. 2002, Christensen et al. 2007); these predictions are consistent with the observed changes in hydrology over the last 50 years (Mote et al. 2005, Stewart et al. 2005). Recent simulations are suggesting that summer temperatures in the western United States are expected

to rise 2 to 5 °C in the next 34 to 63 years (Running 2006) whereas summer precipitation will decline (Christensen et al. 2007). In particular, models and recent evidence indicate that most of Colorado and Utah will develop a climatology in the coming decades in which the levels of aridity encountered during the Dust Bowl of the 1930's or the mid-century drought will become the new standard (Seager et al. 2007). If these forecasts are correct, populations of all trout, including Colorado River cutthroat trout, may be confined to smaller, more upstream habitats affording perennial flow (Keleher and Rahel 1996, Flebbe et al. 2006), potentially including some that are currently uninhabitable because of cold water temperatures (Isaak and Hubert 2004, Cooney et al. 2005). Regional droughts coupled with changes in snowmelt timing could also lead to the synchronous drying of small streams throughout large portions of the Colorado River basin. Given that migration barriers probably restrict the upstream extent of many populations of Colorado River cutthroat trout (cf. Kruse et al. 1997), the overall effect would likely be a net reduction in the abundance and distribution of Colorado River cutthroat trout and an increase in their susceptibility to small-population phenomena such as inbreeding and vulnerability to disturbance. Recent work on disturbance has linked an increase in fire frequency, size, and duration at mid-elevation sites to the earlier snowmelt typical of the last few decades (Westerling et al. 2006); thus, in a warming climate, isolated populations of Colorado River cutthroat trout are likely to be at greater risk from fires and post-fire floods (cf. Brown et al. 2001). This risk may also be high at lower elevations where fire suppression has had the greatest effects on forest stand structure (e.g., ponderosa pine [*Pinus ponderosa*] forests) or where extensive stands of conifers have died from insect attacks (Keane et al. 2002). The probability of intense storms also appears to be increasing (Intergovernmental Panel on Climate Change 2007), and this could heighten the threat of damaging floods. Another risk is that rainbow trout are more tolerant of high temperatures than are cutthroat trout (Bear 2005), which could favor replacement or more rapid introgression of cutthroat trout populations where these species co-occur. It should be pointed out that Colorado River cutthroat trout, and all of the flora and fauna of the Rocky Mountains, have endured climatic conditions more extreme than those at present or likely to exist in the near future (Whitlock et al. 2002). The present cause for concern is that migratory routes to new habitats or persistent refugia have been altered by human water development, barriers to movement, and invasions of nonnative species. Overcoming this problem by relying on human transfers of stocks has a different set of

implications for the persistence of this subspecies that are described elsewhere in this document.

Intentional manipulation of climate, such as cloud seeding to increase winter snowpack, is underway in portions of the range of Colorado River cutthroat trout (e.g., the North Fork Little Snake River basin in south-central Wyoming; Wyoming Water Development Commission, unpublished data). In the absence of overall climate change, such practices might decrease mid-summer water temperatures while increasing base flow in streams with Colorado River cutthroat trout, and they could have positive or negative effects on populations. Predictions regarding current and future outcomes, however, are uncertain because the full magnitude of climate change remains somewhat speculative.

Conservation Status in Region 2

As noted earlier, Hirsch et al. (2006) has provided the most comprehensive assessment of the status of Colorado River cutthroat trout, and these results are summarized below. Primarily because of a variety of anthropogenic events, the distribution, abundance, and diversity of Colorado River cutthroat trout are greatly reduced, relative to historical levels, including on lands administered by Region 2. The majority of populations are restricted to relatively small (<6 km) and/or unproductive headwater (above 2,438 m) streams. Most migratory life history forms have been lost (only 5 percent of conservation populations at least in part retain a migratory life history strategy) and cannot be reestablished in the existing fragmented habitats (about 70 percent of conservation populations are isolated from one another, and strongly connected populations are rare in Region 2). Nonnative trout species now occupy the larger, more productive low-elevation streams and rivers that once supported migratory fish. The many barriers that protect Colorado River cutthroat trout populations from nonnative fish invasions simultaneously isolate them and prevent neighboring populations from providing demographic support or individuals for refounding extirpated populations (Fausch et al. 2006). Extant populations remain at risk from ongoing invasions, barrier failure, or unauthorized human introductions that permit nonnative trout to invade and from catastrophic environmental events that could eliminate individual populations or groups of isolated populations in a basin. It is likely that many populations, particularly the smallest and least productive, are losing genetic variation and that a number of others are introgressed with genes from nonnative congeners. Climate change and a rapidly

growing human population in the Rocky Mountains are likely to exacerbate many of these problems.

Nevertheless, populations of Colorado River cutthroat trout are relatively widely distributed throughout their historical range and in Region 2, so it is unlikely that local environmental phenomena, such as fire or post-fire debris torrents, will threaten considerable numbers of populations at once. In contrast, periodic large-scale environmental events driven by climate change could simultaneously imperil many populations in entire subwatersheds in the Colorado River basin, and result in reduced population sizes that are vulnerable to other effects (e.g., genetic bottlenecks or disturbances to which populations would normally be resilient). Besides fragmenting populations, land and water management have often degraded habitats such that the current abundance of cutthroat trout in some waters is lower than it was prior to Euro American arrival. Chronic disturbances, such as sediment contribution from a variety of land management activities, probably reduce population size and productivity in these already marginal habitats. Land management is unlikely to be the sole cause of wholesale population losses, but in concert with other anthropogenic activities or natural disturbances could tip some populations toward extinction.

Much recent management has been directed at conservation of Colorado River cutthroat trout (Brauch and Hebein 2003, U.S. Fish and Wildlife Service 2004, CRCT Coordination Team 2005, Hirsch et al. 2006, Wyoming Game and Fish Department 2007). Although presently the gains in the overall conservation status of this subspecies are modest, this work has vastly improved the understanding of that status and enhanced the prospects for arresting or reversing declines in some populations, mitigating or reducing threats to others, and establishing or restoring additional ones.

Potential Management in Region 2

Implications and potential conservation elements

Complete restoration of the Colorado River cutthroat trout to its historical range is presently unattainable, largely because invasions of nonnative fish in large systems appear irreversible and habitat loss associated with water diversion is unlikely to be mitigated. Nonetheless, the conservation status of this taxon can be improved in a number of ways. A number of guidelines (see McElhany et al. 2000 and Fausch et al. 2006 for a comprehensive discussion) merit

consideration with respect to ensuring the long-term persistence of populations of Colorado River cutthroat trout throughout their historical range and in Region 2:

- ❖ Replicating indigenous populations in other waters in a particular basin can reduce the risk of loss of unique portions of the genome. This is a commonly recommended tactic for many species of rare salmonids (Apache Trout/Little Colorado River Spinedace Recovery Team 2000, U.S. Fish and Wildlife Service 2003). Increasing the number of populations also reduces the overall risk of extinction of the subspecies.
- ❖ Increasing the size of individual populations beyond particular thresholds (hundreds to thousands of adults; McIntyre and Rieman 1995, Allendorf et al. 1997) can improve the probability of persistence of populations and their retention of genetic variation.
- ❖ Improving habitats could increase productivity and resilience with respect to demographic insults, but it should be recognized that habitats are dynamic and that restoring habitat-forming processes may prove more successful and enduring than altering habitat directly (Beechie and Bolton 1999, Roni et al. 2002).
- ❖ Improving access to stream networks could show increased population persistence because of greater habitat complementarity, availability of refugia, and connectivity to other population segments that might escape deleterious effects of disturbance or management. Populations occupying complex and predictable environments may also be more stable (Schosser 1995, Schlosser and Angermeier 1995). In addition, restoring populations of Colorado River cutthroat trout to basins in different stages of forest succession or different basin configurations reduces the likelihood that a single disturbance, such as a stand-replacing fire or localized downburst, will simultaneously depress all populations (Rieman and Clayton 1997, Miller et al. 2003, Rieman et al. 2003). If such basins are part of the same connected network, habitat complementarity would greatly increase.
- ❖ Restoring larger, more fecund fish with a migratory life history to waters would increase population resilience to habitat alteration from human or natural causes (Rieman and Clayton 1997, Rieman and Dunham 2000), and it might facilitate their persistence despite the presence of nonnative salmonids.
- ❖ Favoring management of wild populations that have the opportunity to evolve may be of critical importance given that the future is uncertain but that change is inevitable (Ruckelshaus et al. 2002). Stated another way, Stockwell et al. (2003) argued that particular populations be viewed not as static repositories of traits but as dynamic reserves of evolutionary potential, or to quote Cox (2004): “The best protection we can give species unique to our land, freshwater, and ocean areas is the potential to adapt by evolution and dispersal to conditions of a rapidly changing environment.” This favors maintaining populations in a wide array of habitats that enable expression of a variety of phenotypes (Healey and Prince 1995) and discourages population maintenance via anthropogenic supplementation (unless conditions become particularly dire; see Minckley 1999). Northcote (1997) contended that management by isolation and periodic supplementation simplified large-scale diversity (Northcote 1997), and some authors (e.g., Willson 1997) consider such isolated populations as evolutionary dead ends (for an alternate view, see Scudder 1989).
- ❖ Introducing this subspecies into formerly fishless waters may harm other organisms (Dunham et al. 2004), and the consequences deserve attention. Other management activities for cutthroat trout, such as the application of toxicants, can also be deleterious for non-target organisms.
- ❖ Defining a strategic, efficient approach to conservation is important because financial and human resources are limited and managers are confronted by an array of decisions about what to do and where to do it (Margules and Pressey 2000). The critical first step of identifying a set of candidate

streams for restoration of Colorado River cutthroat trout has been completed (Hirsch et al. 2006), but rules for prioritizing restoration actions among these have not.

It should be noted that other perspectives on the value of Colorado River cutthroat trout would list a much different set of conservation elements. Quist and Hubert (2004) argued that there appears to be little ecological difference between cutthroat trout and introduced trout species and that the social and economic values of nonnative species usually exceed or at worst are equal to native cutthroat trout. Consequently, they questioned the merit of substantially investing in cutthroat trout conservation beyond maintaining a few token populations given what they perceived to be the inevitable loss of nearly all populations of cutthroat trout. This ignores the legal mandate for conservation of some subspecies of cutthroat trout established by the Endangered Species Act, as well as making evident that it is much less expensive to conserve existing populations than to establish new ones. In addition, there is growing evidence to counter their perspective; for example, it appears that the various salmonid species differentially alter trophic pathways in aquatic and terrestrial ecosystems (Baxter et al. 2005). One thing, however, is certain: the wholesale loss or introgression of indigenous populations of Colorado River cutthroat trout would reroute the course of 5 million years of evolutionary history, and at this point, the outcome is not likely to be appreciated or understood (for a similar perspective with respect to brown trout, see Araguas et al. 2004). Consequently, preserving the potential for all foreseeable conservation alternatives appears prudent.

That said, it should be acknowledged that the success of Colorado River cutthroat trout conservation may have less to do with tactics and strategies than with cultural values and the flexibility and openness of biologists, agencies, and the public to new solutions. Lichatowich et al. (1999) pointed out that as early as the 1880's, as a society we understood what caused declines in salmon populations in the Pacific Northwest, yet many of these populations were subsequently decimated or extirpated. They argued that this resulted from an inherent societal belief in a harvestable excess, faith in the efficacy of technological solutions for ecological problems, and an unwillingness to recognize signs of failure because of an ideological certainty in the correctness of a particular solution. For these reasons, they doubted that many biologically focused management proposals would improve prospects for Pacific salmon. Along the same lines, Lackey et

al. (2006) related that fisheries professionals often expressed public optimism about salmon recovery efforts but were privately pessimistic, and they concluded that these professionals recognized that efforts at salmon conservation were destined to be futile without policy and institutional change. One such change might be to practice adaptive management (Walters 1986), a style of resource management that emphasizes learning by doing, but despite much fanfare, it has not been widely adopted or consistently applied with success (Ludwig and Walters 2002, Sabine et al. 2004, Stankey et al. 2005). Allan and Curtis (2005) believed that resistance to adaptive management, with its emphasis on reflection, learning, and embracing complexity, arose from existing management styles that favor activity, control, comfort, and certitude about outcomes (also see McAlpine et al. 2007). Minns et al. (1996) reached a similar conclusion with regard to fish habitat restoration, in that to some agencies it was more important to be seen doing something than it was to try to understand the correct thing to do. Nevertheless, the partial successes in some case studies of adaptive management (i.e., improved integration between management concerns and research priorities and greater appreciation of the critical role of monitoring) illustrate its potential value for addressing complex ecosystem management problems (Bormann et al. 2007). Regardless of the approach, experimenting with institutional change warrants consideration equal to that given to the application of particular strategies or adoption of protocols in the conservation of Colorado River cutthroat trout in Region 2.

Tools and practices

Population and habitat monitoring

A review of the literature indicates that there is a burgeoning interest in statistically sound, politically necessary, and ecologically meaningful monitoring programs (e.g., Fitzpatrick et al. 1998, Urquhart et al. 1998, Kaufmann et al. 1999, Stevens and Olson 1999, Williams et al. 2002). Also abundant are critiques arguing that most monitoring designs are neither robust nor relevant, rendering them almost useless (e.g., Bisbal 2001, Yoccoz et al. 2001, Legg and Nagy 2006). Because adequate inventorying and monitoring is fundamental to identifying the location, extent, and size of fish populations, the kind and amount of habitat, and the variation and trends in both, the importance of their thoughtful development cannot be exaggerated.

Bisbal (2001) offered a seven-step outline for developing a sound monitoring program for fish and

wildlife in the Columbia River basin (see Thompson et al. 1998 for a more generic though comprehensive review of monitoring). These steps include:

- 1) adopt an ecological management framework that integrates an agency vision for a species and its ecosystem in the context of society and natural events
- 2) identify what could be monitored (e.g., any characteristic of a Colorado River cutthroat trout population or its habitat) and at what scale (e.g., range-wide, region-wide, or forest-wide) to achieve this vision
- 3) establish what will be monitored (i.e., what subset of possible indicators will provide the essential information on the status of the species and ecosystem of concern, what design best captures that information, and what thresholds will trigger a management response) and performing a pilot study to validate the selections
- 4) create a data archive that captures what is already being done and what should be added
- 5) procure that additional information
- 6) manage the data by ensuring that quality control and assurance are practiced, and keep the data accessible, formatted for ready analysis, and regularly updated
- 7) conduct three forms of evaluation:
 - a) scientific evaluation to ensure that the monitoring system is valid and the data are credible
 - b) policy evaluation to determine whether the data are sufficiently informative to make management decisions, which may lead to changes in objectives as well as the monitoring strategy
 - c) public evaluation, including review of the data and inclusion in decision making, to promote accountability of managers and politicians.

A full discussion of all aspects of a sound monitoring program for Colorado River cutthroat trout is beyond the scope of this manuscript. However, the conservation strategy for Colorado River cutthroat trout (CRCT Conservation Team 2006b) specifies that

several types of monitoring will be conducted, and these points are discussed in greater detail below.

Population inventory: Although an understanding of the distribution of many lesser-known fishes in this region would benefit from predictions based on statistical models of habitat (Angermeier et al. 2002, Olden and Jackson 2002), the inventory of populations of Colorado River cutthroat trout is probably approaching completion because this taxon has been the subject of focused efforts for decades. Although Behnke and Zarn (1976) knew of only two genetically pure populations of Colorado River cutthroat trout in its entire range, later surveys by Binns (1977), Remmick (1982) Oberholtzer (1987, 1990), Martinez (1988), and others have noted the locations of hundreds of populations. Previously undiscovered populations continue to be found (H. Sexauer, Wyoming Game and Fish Department, unpublished data, D. Renner, Arapaho-Roosevelt National Forest, unpublished data), but these are often in waters once thought too small, steep, or isolated to contain Colorado River cutthroat trout. Consequently, these and any remaining unreported populations are likely to be small, but they may constitute novel components of the genomic diversity of this taxon.

The location of populations has usually relied on developing a list of streams with suitable environmental characteristics (i.e., likely trout streams) that were not believed to have been invaded by nonnative salmonids or to have been stocked, followed by field surveys relying on observations from stream banks or spot samples with electrofishing (Hepworth et al. 2001, Colorado Division of Wildlife and Wyoming Game and Fish Department, unpublished data). These surveys are typically informal and provide semi-quantitative information on the size, structure, and longitudinal distribution of individual populations. More structured sampling that facilitated predictions about presence and habitat relations has been conducted for other salmonids in the Rocky Mountains (Paul and Post 2001, Rich et al. 2003), and still more rigorous inventories have been proposed (Peterson et al. 2002).

There have been many inventories of the genetic status of Colorado River cutthroat trout populations (Hirsch et al. 2006). These surveys were generally conducted to evaluate the level of introgression of Colorado River cutthroat trout populations with nonindigenous *Oncorhynchus*. Because of the costs of analyses or risks to the population from lethal sampling for allozyme studies, such sampling has been less comprehensive than population detection or

monitoring. Sampling is becoming more commonplace because the techniques currently available to evaluate mitochondrial, ribosomal, and nuclear DNA are increasing the probability of detection of introgression (primarily due to the increase in diagnostic markers and ability to use non-lethal tissue samples; Neville et al. 2006b) while reducing the expense of analyses and effects on sampled populations. One caution is that populations can never be conclusively demonstrated as being free from introgression. Instead it can be stated that with a given level of confidence, the percentage of nonindigenous genes is below some value (e.g., there is a 95 percent probability that the proportion of rainbow trout genes present is ≤ 1 percent) with the caveat that these values will vary based on which method is used and what part of the genome is examined (Pritchard et al. 2007a). A second issue is that sometimes little attention is given to the spatial distribution of fish sampled for genetic analyses. Fish collected from a single site may be unrepresentative of the entire population (Bischoff 1995, Weigel et al. 2003).

Population monitoring: As alluded to above, how population monitoring is conducted should reflect why monitoring is needed. For example, objectives that involve understanding population size, structure, distribution, trend, response to management, variability, synchrony, or probability of extinction (Thompson et al. 1998, Staples et al. 2005) could dictate different forms of population monitoring. An objective of the conservation strategy for Colorado River cutthroat trout (CRCT Conservation Team 2006b, p. 13) is to “identify all waters with CRCT populations and monitor known populations to detect changes,” which implies that the number of populations and size of habitats will be important targets of a monitoring scheme. Furthermore, a key strategy within the conservation strategy is to “continue monitoring CRCT populations, with emphasis on accurate assessment of total adult cutthroat populations and relative abundance of native non-game species...” (CRCT Conservation Team 2006b, p. 14). Collectively, these statements indicate that monitoring must be sensitive enough to identify population trends, but they do not state the magnitude of change to be detected or over what interval. In addition, given that the required sampling needs to be adequate to gauge population size, a relatively high degree of precision is also presumably desired.

Presently, most quantitative population monitoring of Colorado River cutthroat trout in Colorado and Wyoming is based on periodic sampling (e.g., every 4 to 5 years, of one to a few index reaches in selected streams. Index reaches tend to be about 100 m long,

and block nets are sometimes installed at each end of the index reach during sampling. Crews typically make two or three electrofishing passes and use estimators based on the removal method to calculate abundance of juvenile and adult fish, but not of age-0 individuals (Colorado Division of Wildlife and Wyoming Game and Fish Department, unpublished data).

Measuring in-stream distribution: Most current inventories of Colorado River cutthroat trout do not appear to address their within-stream distribution. Yet knowledge of the upstream-downstream boundaries of a population is crucial if abundance estimates are extrapolated from sampled reaches. In some areas, whether or not particular stream reaches harbor fish affects management of adjacent riparian and upland forests (Cole et al. 2006). Biologists have devised a number of methods to estimate the longitudinal distribution of inland trout populations within streams. Harig and Fausch (2002) identified the extent of greenback cutthroat trout in study streams by walking upstream from a known fish barrier while observing fish from the stream bank or probing cover to disturb concealed individuals, an effective procedure because cutthroat trout tend to be active and visible during the day (Young 1996). They ceased observations upon encountering an obvious fish barrier or stream channel so narrow (≤ 1 m wetted width) that the numbers of cutthroat trout present, if any, would not be appreciable (Harig and Fausch 2002). Occupied stream length was then measured with a geographic information system. Young and Guenther-Gloss (2004) and Young et al. (2005) used a similar visual method to define the downstream-upstream limits of populations of greenback cutthroat trout or Colorado River cutthroat trout, but measured channel length in the field with a drag tape. They also continued visual observations for 500 m past the last fish detected or until wetted stream width was ≤ 0.5 m. This was followed by electrofishing at systematic intervals (usually ≈ 250 m) to verify conclusions about trout distribution. Similar approaches for assessing inland trout distributions have been used elsewhere (Propst and Stefferud 1997, Jones et al. 1998, Sloat et al. 2002, Bateman et al. 2005, Cole et al. 2006). It should be recognized that trout populations may contract or expand their upstream or downstream limits depending on environmental conditions (Larson et al. 1995, Jones et al. 1998), but these shifts tend to be relatively minor for fish with resident life histories (Cole et al. 2006, Fransen et al. 2006, but see Clapp et al. 1990 and Colyer et al. 2005 for an example of how the timing of sampling would influence estimates of downstream limits). In addition, barriers and other unsuitable environments can restrict populations to a fraction of

the available perennial stream habitat (Angermeier et al. 2002, Wofford et al. 2005), so map-based estimates (Fransen et al. 2006) in lieu of field surveys are unlikely to be reliable.

Measuring in-stream abundance: Three techniques are frequently used to count trout: stream bank observations, snorkeling, and electrofishing. In general, stream bank counts are the least robust because large numbers of fish are not detected and detection depends on fish behavior and viewing conditions (Heggenes et al. 1990, Bozek and Rahel 1991a, Young and Guenther-Gloss 2004, Young et al. 2005). As noted above, however, visual counts have been helpful in describing fish distributions (Harig and Fausch 2002) and are less labor intensive than other methods. Nighttime spotlighting has also been effective (Hickey and Closs 2006), but visibility depends on fish behavior and habitat complexity. Snorkel surveys have been widely used for estimating fish abundance (e.g., Mullner et al. 1998, Wildman and Neumann 2003), and protocols for effective sampling have been described (Dolloff et al. 1996). Counts obtained during day or night snorkeling sometimes differ substantially, with counts at night often being much higher in streams with cold temperatures (Roni and Fayram 2000, Thurow et al. 2006). Although snorkel counts of many species tend to be less than those obtained by electrofishing (Rodgers et al. 1992, Thurow and Schill 1996, Thurow et al. 2006), these are often correlated, and snorkeling may be favored because it requires less effort (Hankin and Reeves 1988, Roni and Fayram 2000).

Electrofishing is the most widely used method for obtaining counts of Colorado River cutthroat trout to obtain abundance estimates. The basics and nuances of proper technique have been thoroughly addressed (Bohlin et al. 1989, Cowx 1990, Cowx and Lamarque 1990), although approaches for optimizing effectiveness are still being developed (Miranda and Dolan 2003, 2004, Beaumont et al. 2005, 2006). Despite that electrofishing usually generates greater counts than other methods, not all fish are caught because the vulnerability to capture varies with fish length (Zalewski 1985, Dolan and Miranda 2003, Peterson et al. 2005), habitat complexity (Peterson and Cederholm 1984, Habera et al. 1992), habitat size (Riley et al. 1993, Rosenberger and Dunham 2005), water depth (Gardiner 1984), conductivity (Zalewski and Cowx 1990), fish species (Peterson et al. 2004b), fish density (Kruse et al. 1998), and whether an area has recently been electrofished (Cross and Stott 1975, Riley and Fausch 1992). This variation in capture efficiency has important ramifications for obtaining unbiased estimates of trout

abundance, depending on the estimator that is used, but high capture efficiencies are necessary for precise estimates regardless of model choice (White et al. 1982). This must be balanced with the risk of injury to some fraction of the fish population (Reynolds 1996, Barton and Dwyer 1997, Snyder 2003), particularly of rare or federally listed species (Nielsen 1998).

The two most commonly used estimators are removal (or depletion) estimates and mark-recapture (also known as Petersen or Lincoln-Petersen) estimates (Seber 1982, Gatz and Loar 1988, Williams et al. 2002). Removal estimates are based on the notion that a constant effort will result in a constant rate of removal (i.e., the number of fish removed on each sampling pass is a fixed proportion of those present). The accuracy of removal estimates relies on meeting several assumptions:

- 1) for all practical purposes, the population is closed (i.e., there are no births, deaths, emigrants, or immigrants) during sampling
- 2) all fish have an equal probability of capture
- 3) probability of capture remains constant during all sampling intervals.

Mark-recapture estimates consisting of a single marking run and recapture run, as practiced by most stream biologists wishing to obtain an abundance estimate, also depend on (1) and (2) above, and that all marked individuals are recognized.

To meet the first assumption, biologists have sometimes installed block nets at the upstream and downstream ends of sampling reaches to prevent fish from escaping during sampling. However, many biologists forego using block nets because they do not believe that many fish attempt to swim a great distance to avoid capture, that numbers of escaping fish are low relative to total numbers of fish present, and that installation of block nets may cause fish to flee from or into the sampling area and bias capture totals (Bohlin et al. 1989, Amiro 1990a, Heggenes et al. 1990). Peterson et al. (2005) demonstrated that substantial numbers of bull trout and rainbow trout moved during electrofishing and advocated that block nets be used, but they noted that movement (or the lack thereof) of rainbow trout was explained more by the presence of rubble on the stream bottom than the presence of a block net. In contrast, Young and Schmetterling (2004) found that very few fish left 200-m sampling sections between mark and recapture runs, and that ignoring

fish movement would have resulted in positive biases in abundance estimates of 3 to 8 percent. Regardless, the installation of block nets represents a substantial investment in time and labor that might cause crews to forego additional sampling. This tradeoff, and defining *a priori* an acceptable level of this sampling bias, may be important to a monitoring plan.

The second assumption of equal catchability among all individuals has long been known to be false because electrofishing is a size-selective technique. Consequently, biologists usually develop separate population estimates based on the catchability of fish of different lengths (Büttiker 1992) or forego estimates of fish below a given size (for example, age-0 fish). More problematic is the implicit assumption that the catchable population equals the total population. Bohlin and Sundström (1977) suggested that some proportion of the population could avoid capture based on physiology or behavior, and that these fish were not visually distinguishable from other members of the population. It is difficult to correct for this bias in population estimates, which can also be generated by unequal catchability among marked and unmarked fish (such as from a nonrandom distribution of each or inherent differences in vulnerability to electrofishing; Peterson and Cederholm 1984). Heterogeneity in capture among individuals can be incorporated into more sophisticated models (Williams et al. 2002), but these are rarely used for routine population estimation.

The assumption of equal detectability during all sampling intervals is the most difficult to meet. Recently electrofished trout undergo physiological and behavioral changes for about 24 h that may render them less vulnerable to recapture by electrofishing (Mesa and Schreck 1989). To overcome this problem, biologists may wait several hours to several days between mark and recapture runs (Vincent 1983, Rodgers et al. 1992, Peterson et al. 2004b, Rosenberger and Dunham 2005, Temple and Pearsons 2006). However, those performing multi-pass removal estimates often repeat sampling passes at much shorter intervals (=1 h), which appears to reduce catchability of fish on successive passes (Riley and Fausch 1992, Peterson et al. 2005). The resulting negative bias in removal estimates is sometimes severe (> 50 percent) and has long been recognized (Cross and Stott 1975, Heggberget and Hesthagen 1979, Mahon 1980, Bohlin 1982, Amiro 1990b, Libosvářský 1990). Consequently, mark-recapture methods tend to estimate abundance more accurately than do removal methods (Peterson and Cederholm 1984, Rosenberger and Dunham 2005). However, these estimates also suffer from bias when model assumptions are not met

(Robson and Regier 1964, White et al. 1982, Peterson and Cederholm 1984). Whichever model is chosen, greater capture efficiency and greater effort typically results in more precise and less biased estimates (Robson and Regier 1964, Randall 1990, Rosenberger and Dunham 2005).

A more fundamental issue with monitoring populations of Colorado River cutthroat trout may be dealing with spatial variation in abundance. Although extrapolating counts or estimated abundance from single (or a few) reference, representative, or index reaches to entire streams is typical, the method lacks inferential power because of the untenable assumption of uniform fish densities throughout a stream (Thompson et al. 1998, Yoccoz et al. 2001, Williams et al. 2002, Williams et al. 2004). Many studies have demonstrated high spatial variation in abundance in salmonid populations (Jones et al. 1998, Mitro and Zale 2000, Young and Guenther-Gloss 2004), even among adjacent reaches (Amiro 1990b). Consequently, sampling from the entire occupied portion of a stream channel is essential to estimate fish abundance accurately because it addresses spatial heterogeneity in abundance and defines the boundaries of occupied habitat (Hankin and Reeves 1988, Dolloff et al. 1993).

Limited budgets and time have caused biologists to seek methods that produce sufficiently precise abundance estimates yet capture the spatial heterogeneity in populations. Foremost among these in recent years is the basinwide inventory (Hankin and Reeves 1988, Dolloff et al. 1993), which relies on double sampling and a spatially comprehensive, systematically drawn sample of habitat units. All selected units are censused with a less precise technique, such as snorkeling or single-pass electrofishing, and counts from these units are calibrated by comparing them to counts obtained with a more precise method, such as multi-pass electrofishing, from a subsample of these units. The number, kind, and size of sampling locations is predicated on acceptable levels of precision in abundance estimates (Hankin and Reeves 1988, Thompson et al. 1998, Young and Guenther-Gloss 2004). In general, the use of calibrated single-pass electrofishing catches as an index of whole-stream population abundance is gaining popularity (Strange et al. 1989, Lobón-Cerviá and Utrilla 1993, Jones and Stockwell 1995, Jones et al. 1998, Kruse et al. 1998, Wyatt 2002, Young and Guenther-Gloss 2004, Young et al. 2005). Nevertheless, this approach still suffers from the negative bias associated with abundance estimators, particularly that attributable to environmental variability in catchability (Thompson 2003, Peterson et al. 2004b, Rosenberger and Dunham

2005, Sweka et al. 2006). However, spatial variation in abundance may vastly outweigh imprecision or bias associated with estimates at particular sites (Mitro and Zale 2000, Bateman et al. 2005). Because obtaining highly precise and accurate abundance estimates from large portions of individual streams is time consuming and expensive, quantifying and balancing these different sources of error will be essential to constructing a defensible yet practical approach to gaining reliable information on population size.

The point of many monitoring schemes is to detect temporal variation in terms of population trends, overall fluctuation, or synchrony. A vital issue for managers is the period of monitoring that may be necessary to detect a change in population size, which is contingent on the precision of population estimates, the temporal fluctuation in abundance, the magnitude and direction of change to be detected, and the level of confidence one hopes to have in the prediction (Peterman 1990, Thompson et al. 1998). For example, in a recent assessment on detecting trends in bird populations in North America, Bart et al. (2004) recommended a monitoring scheme that yielded 80 percent power to detect a 50 percent decline within 20 years based on annual monitoring, noting that detecting smaller declines at shorter intervals was impractical. The few attempts to assign specific values to each of these variables for salmonid populations have not been encouraging. For example, it may require decades to detect even very large changes in population size (Korman and Higgins 1997, Maxell 1999, Ham and Pearsons 2000, Maxwell and Jennings 2005), mainly because of the high temporal variability in abundance (also see Platts and Nelson 1988 on salmonids and Peterman and Bradford 1987 on marine fishes). In general, the power to detect a change will decrease as the size of the change decreases, the imprecision or variability in abundance estimates increases, and the interval of observation and number of censuses decreases. In addition, annual sampling of permanent monitoring stations may be more efficient at detecting changes than random annual allocations of sites (Quist et al. 2006). However, the underlying assumptions of such monitoring schemes are that salmonid populations decline proportionally throughout occupied habitats or that adjacent waters will have populations that fluctuate synchronously, which may or may not be true (Rieman and McIntyre 1996, Pess et al. 2002, Isaak and Thurow 2006; for a nonsalmonid example, see Shackell et al. 2005). Either way, this has important ramifications for the distribution of monitoring sites or streams to detect trends (Strayer 1999, Jonzén et al. 2005). A final consideration is weighing the levels of risk and cost that

are acceptable (i.e., is it more important to respond to apparent trends and accept the cost of acting when it may not be necessary, or is it worthwhile to be more certain about even very small changes that demand large investments in monitoring? [Legg and Nagy 2006]) In addition, it may be more important to detect population declines rather than increases because the former may warrant management intervention (e.g., Maxwell and Jennings 2005). Because of these difficulties and the uncertainties associated with abundance estimates, Staples et al. (2005) favored monitoring based on estimating risks to populations, but this strategy relies on the existence of a comprehensive, long-term data set to gauge risk quantitatively, a luxury that is probably lacking for most populations of Colorado River cutthroat trout.

Many of these population monitoring issues may also apply to other characteristics of Colorado River cutthroat trout populations, such as size structure and demographic parameters (Kritzer et al. 2001, Vokoun et al. 2001) or year class strength (Cowx and Frear 2004), but these have not been explored. Because a goal of the conservation strategy for Colorado River cutthroat trout is to ensure that “the genetic diversity of the species is maintained” (CRCT Conservation Team 2006b, p. 13), a critical addition may be the monitoring of genetic characteristics of Colorado River cutthroat trout, such as population genetic structure (Nielsen and Sage 2001, 2002), the geographic distribution of genetic variation among and within populations (Wenburger and Benson 2001, Wofford et al. 2005), or historical and current gene flow (Neville et al. 2006a). Schwartz et al. (2007) suggest some guidelines for genetic monitoring.

Habitat inventory and monitoring: The Colorado River cutthroat trout conservation strategy proposes comprehensive monitoring of watershed conditions, stream and lake habitats, instream flows, lake levels, and water quality, in some cases to ensure optimum long-term conditions or that there are no adverse effects from land management (CRCT Conservation Team 2006b, p. 17-18, 20). A successful inventory and monitoring strategy tailored to meet these ambitious goals will be challenging. For example, an ideal variable for detecting trends in and describing quality of physical habitats would be one that has a strong influence on fish population size or viability, may be altered by management activities or disturbance, has little inherent within-stream spatial or temporal heterogeneity, and can be measured without error and at little cost. Other than perhaps the presence or absence of water, such a variable does not exist; consequently, this has contributed to the development of an extensive

literature on habitat inventory and monitoring (e.g., Dolloff et al. 1993, Overton et al. 1997, Fitzpatrick et al. 1998, Urquhart et al. 1998, Bain and Stevenson 1999, Kaufmann et al. 1999, Stevens and Olson 1999, Peck et al. 2001, Reeves et al. 2003a, Henderson et al. 2004, Hixon et al. 2004, Larsen et al. 2004). Much of this literature has targeted salmonid habitats and is summarized elsewhere (Roni 2005, Stalnack et al. 2005). Consequently, this discussion will only touch on some of the major points.

Vast arrays of habitat variables that are presumably biotically relevant have been included in monitoring schemes for salmonids. Quite problematic, however, is the lack of a quantitative understanding of the relation between trout abundance (and population viability) and these habitat characteristics (including their range and dynamics), which leads to ambiguity in the apparent response of populations to habitat changes other than the most obvious ones (cf. Bryant et al. 2005, Rosenfeld and Hatfield 2006). For example, because low water temperature appears to play a strong role in controlling the year class success of high-elevation populations (Harig and Fausch 2002, Coleman and Fausch 2007a,b), it may be a key variable for monitoring and may be sensitive to management and natural disturbance. In contrast, the abundance of pools, despite their importance to Colorado River cutthroat trout and greenback cutthroat trout (Young 1996, Harig and Fausch 2002), were poorly correlated with abundance compared to the length of occupied channel (Young et al. 2005).

Many variables are routinely monitored to assess the effects of management activities or natural disturbance. However, detecting changes attributable to these factors is contingent on two properties: 1) that the magnitude of change of a habitat component exceeds its inherent variability and the error associated with its measurement, and 2) that the habitat component responds in a predictable way. Assessments that have sought variables satisfying these requirements have found the list to be surprisingly short (Kaufmann et al. 1999, Archer et al. 2004). In some cases, variables were associated with high amounts of observer error (e.g., the percentage of fine sediment, or the size, number, or depth of pools; Poole et al. 1997, Roper et al. 2002, Williams et al. 2004), high within- and among-stream variability (e.g., large wood counts; Archer et al. 2004, Young et al. 2006), or both (e.g., several measures of riparian vegetation; Coles-Ritchie et al. 2004, Henderson et al. 2004). Even within a limited set of variables, some respond in surprising ways. Kershner et al. (2004) surveyed reaches of over 250 streams

throughout the interior Columbia River basin, and they found significant differences between managed and reference sites for eight of 12 variables. Predictably, residual pool depths and measures of bank stability and undercut were greater in reference streams, but contrary to expectation, the median particle size was also lower. In addition, there was no difference in the percentage of pools between managed and reference sites, despite that this difference had been observed elsewhere in the basin (McIntosh et al. 2000). They attributed this discrepancy in part to the absence of large wood in most of their monitoring reaches (because riparian zones adjacent to monitored reaches were infrequently forested; Kershner et al. 2004), which emphasizes how site selection and geomorphic position can shape the outcome of a monitoring plan (Montgomery and MacDonald 2002).

Monitoring schemes must be scaled to satisfy the objectives of monitoring (Williams et al. 2004). The whole-basin monitoring protocols for addressing objectives of the Northwest Forest Plan and PACFISH/INFISH effectiveness monitoring are designed to detect changes at scales of entire river basins or geographic regions (Reeves et al. 2003a), but they might be successful at detecting changes across smaller landscapes such as individual national forests as long as sampling intensity is high (e.g., 35 to 90 sampling sites) (Henderson et al. 2004; see Larsen et al. 2004 for a similar suggestion). If the objectives are to detect meaningful stream- or site-specific trends, more intensive sampling within and among streams, often at permanent sample sites, of variables likely to respond to particular management activities will be necessary (Archer et al. 2004, Kershner et al. 2004), and in many cases these standards will be difficult to achieve. Regardless of the protocol followed, there is consensus that extensive training is essential to produce reliable results (Roper and Scarnecchia 1995, Henderson et al. 2004).

Population and habitat management approaches

Habitat improvement: The physical manipulation of streams to improve fish habitat, stream channel and riparian stability, and water quality are common practices throughout the United States, with annual expenditures exceeding \$1 billion (Bernhardt et al. 2005). Those wishing to install structures or rework stream channels can find extensive guidance in the literature (e.g., Hunter 1991, Jenkinson et al. 2006). Although remediation of point sources of habitat or population degradation (e.g., screening irrigation ditches, restoring fish passage where culverts prevent

access to suitable habitat, rebuilding meanders in artificially straightened channels, shading devegetated banks, or halting sediment contributions from road surfaces) can have readily discernable immediate and long-term benefits, the addition of in-stream habitat structures, even when apparently successful (Binns et al. 2004), is more problematic (Independent Scientific Advisory Board 2003).

Several of the kinds of structures used today were first designed in the 1930's (Thompson 2006). Many of these have relatively short working lives because flows often damage them or make them ineffective (Frissell and Nawa 1992, Thompson 2006). Even when structures persist and appear to be functioning, they may lead to unintended consequences. For example, Cowx and van Zyll de Jong (2004) reported that in a log-driven Canadian stream, habitat structures were added with the goal of increasing the abundance of brook trout. Brook trout did not become more abundant in response to these installations, but a competitor, juvenile Atlantic salmon (*Salmo salar*), did. Gowan and Fausch (1996) concluded that increases in trout abundance associated with log-drop structures in Colorado streams were probably attributable to redistribution, not increases in population size. Moreover, Thompson (2006) argued that the greater angler catch rates often associated with structures reflected both a redistribution of fish and an increase in angler effort, which actually led to net declines in overall fish abundance; in essence, structures became ecological traps for trout attracted to them.

Typically, fish-related habitat improvement assumes that we know which factors limit fish populations in a given location and that artificially manipulating habitat composition will relax the limitations and increase fish abundance. A critical problem is that it is difficult to verify these assumptions because of the rarity of post-project monitoring (Bash and Ryan 2002, Bond and Lake 2003, Reeve et al. 2006). In two cases where extensive monitoring was conducted, the authors concluded that the factors limiting fish abundance were not addressed because either they were misidentified or were upstream or downstream of the habitat improvement area (Reeves et al. 1997, Ward 2000). In addition, the absence of untreated control streams weakened any inferences that could have been drawn (Independent Scientific Advisory Board 2003).

As alluded to above, many questions related to spatial scale and stream management remain to be answered (Jensen et al. 2001). Fausch et al. (2002) contended that many researchers and managers have

neglected to appreciate the scale of habitats at which trout perceive their environment and have questioned whether we can manage habitats at that scale. The grain (i.e., the smallest habitat unit of relevance) and extent (the size or spatial distribution of these habitats) to which trout respond are probably inherent properties (Fausch et al. 2002). Moreover, combining these with variation in environmental quality can contribute to the spatial heterogeneity in abundance (Schooley 2006), and these patterns in salmonids have only recently come under scrutiny (e.g., Torgersen et al. 2004, Ganio et al. 2005).

Because of our incomplete understanding of the relations between habitat characteristics and cutthroat trout abundance, it may be simpler and more biologically defensible to increase the amount of habitat available to fish by increasing the length of stream that a population can occupy (e.g., move existing anthropogenic barriers farther downstream) rather than by altering instream habitat, and to favor the restoration of natural processes or the cessation of damaging activities throughout an entire watershed, which will enable habitat appropriate for a particular system to develop (Beechie and Bolton 1999, Reeve et al. 2006). Although a biologist familiar with stream restoration and our desire to effect change once quipped "for most Americans, instant gratification isn't fast enough" (also see Minns et al. 1996 for a similar position, and Reeve et al. 2006 on how the way that funding has been awarded reinforces this shortcoming), a longer-term, larger-scale perspective on habitat restoration may ultimately be more successful. Again, a review of individual tactics or best management practices is beyond the scope of this paper, but examples range from the large-scale buyout of federal grazing leases or changes in grazing systems that diminish livestock effects to the site-specific reduction in water losses in irrigation canals by installing pipe (and the negotiated return of the water savings to salmonid spawning and rearing streams).

Increasing habitat size or stream network connectivity can have an additional benefit - the restoration of migratory populations of cutthroat trout. Swanberg (1997), Schmetterling (2003), and Schmetterling and McFee (2006) transported mature bull trout, westslope cutthroat trout, and largescale suckers (*Catostomus macrocheilus*) over a dam on the main-stem Clark Fork River in Montana that had been impassable to upstream migrants for over 90 years, and they found that these individuals moved long distances (up to 100 km) to reproduce in what were presumably their natal waters. This suggests that despite isolation that selected against such migrants for

tens of generations, this life history form was still extant in these populations (although elsewhere extirpation of mobile forms has resulted; Nelson et al. 2002).

Nonnative species: prevention of invasions:

Although habitat degradation can depress or extirpate a fish population, it has the advantage of occasionally being reversible. In most cases, invasions by nonnative fishes are not, and preventing invasions is far easier than attempting to manage them. Unfortunately, the simplest form of prevention – not introducing nonnative fish in the first place – has been rendered moot by over a century of agency-sponsored and publicly supported sport-fish stocking, and the subsequent spread and establishment of these fishes. Although stocking of nonnative fish within the historical range of Colorado River cutthroat trout continues, this practice has effectively ceased in waters that contain remnant or reintroduced populations (Hirsch et al. 2006). More problematic recently has been the redistribution of nonnative fishes by members of the public (Rahel 2004). In several instances, the appearance of nonnative trout above apparently functioning fish migration barriers has been attributed to such illegal introductions (U. S. Fish and Wildlife Service 1998, M.K. Young, unpublished data). This practice threatens conservation work that often required hundreds of hours of labor and tens of thousands of dollars, yet prosecution of offenders is virtually impossible because of the ease of committing these transgressions and the limited law enforcement presence on public lands. Where feasible, one strategy could be to limit motorized access near some waters, particularly near barriers, by closing or rerouting roads; it appears less likely that nonnative fish would be transported alive over long distances by hand. A more draconian measure would be to establish refuges closed to fishing, with the belief that this would reduce public desire for fishing in those waters and perhaps the probability of transfer of pathogens on fishing equipment. However, this could produce a public backlash that might result in targeting those waters for nonnative introductions and reduce support for conservation activities.

Legal introductions of nonnative fish by private entities, such as for recreational fishing ventures, also represent a risk to conservation efforts. This is a likely pathway for the introduction of new pathogens (see Parasites and diseases, above), particularly if cultured fish can be released into waters that permit them to mix with wild populations. In one case, a natural waterfall that had been effective in repelling nonnative trout (and native mountain whitefish) from moving upstream among a population of Colorado River cutthroat trout was scaled when a private landowner downstream

stocked and grew outsized rainbow trout that were able to leap over the falls (Medicine Bow-Routt National Forest, unpublished data).

The primary tactic for halting an invasion, or preventing reinvasion of habitats from which nonnative fish have been removed, is the installation of a barrier. Fausch et al. (2006, and references therein) exhaustively consider the consequences of intentional isolation as a management strategy, as well as describing the effects of nonnative salmonid invasions on native salmonids and the issues that should be addressed when considering the tradeoff between invasion and intentional isolation. The remainder of this discussion will highlight some aspects of prophylactically managing nonnative species.

In some streams, natural barriers in the form of waterfalls, cascades, bedrock chutes, or even subterranean reaches may already exist (whether waters upstream of such features constitute historical habitat is considered below). In the absence of a natural barrier, installation of an artificial one is an alternative, albeit an expensive one. Costs to install barriers to protect Apache trout in small (3 to 12 m) streams in Arizona ranged from \$150,000 to \$3,000,000 (Avenetti et al. 2006). Specifications for a wide array of barriers being used to impede upstream migrations of nonnative fish are available elsewhere (Hepworth et al. 2002, <http://wildfish.montana.edu/projects/barrier/browse.asp>) and will not be discussed further. However, the presence of an artificial barrier is no assurance that an invasion of nonnative fish will be averted. Harig et al. (2000) found that nearly all structures built to stop invasions of nonnative fishes into streams occupied by greenback cutthroat trout had eventually been breached by nonnative fish.

Artificial barriers fail for a number of reasons. In some cases, they are porous or too short, or they developed a jump pool that enabled nonnative fish to scale them (also see Thompson and Rahel 1998). Barriers may also fail because they are ill-designed for the hydraulic characteristics of a site. Outright collapse or partial destruction of barriers, usually during high flows, is common (M.K. Young, personal observation). Such barriers are often undersized for the locations where they are installed, or better sites for construction (i.e., channels confined between hillslopes of exposed bedrock) were not available or were overlooked. In one case, a barrier consistently failed not because it was damaged but because bedload transport aggraded the channel and obliterated the nick point (M.K. Young, personal observation). Nevertheless, installation of new barriers is widespread (Wyoming Game and

Fish Department 2007); it is hoped that more recently constructed barriers will be more successful.

An alternative to new barrier construction may be the use of an existing barrier installed for another purpose. Although some (e.g., culverts) are prone to being washed out during relatively modest floods, others (e.g., diversion structures designed to capture water for agricultural and municipal use) are constructed to higher engineering standards than those designed by biologists. Some diversions already function as barriers and others might be retrofitted to do so. If reauthorization for these must be granted periodically by a federal agency, then additional construction could be recommended as part of that process.

Regardless, even the best-designed and best-placed barrier will require regular maintenance for the life of the structure; estimated annual repair costs of the aforementioned structures in Arizona was \$3,000 to 15,000; Avenetti et al. 2006). In addition, they will be likely to fail during extreme events such as debris torrents. All things considered, an artificial barrier should be regarded as a stopgap measure; ultimately, the only permanent method for securing populations of Colorado River cutthroat trout will be the removal of nearby nonnative trout populations and reestablishment of connectivity to larger stream networks (Hepworth et al. 2002).

Nonnative species: removal and control:

Because nonnative trout species appear to preclude the reoccupation of many waters by Colorado River cutthroat trout, removal of these species has been a priority. The number of techniques available, however, is fairly limited, and new approaches have not developed beyond the experimental stage (e.g., pheromone-based removals of brook trout; Young et al. 2003). Probably the most popular approach is chemical treatment with rotenone or antimycin, which have a long history of use in the western United States. Since that time, toxicants have been repeatedly administered to remove nonnative trout from waters prior to the introduction or reestablishment of trout species native to these basins (Rinne et al. 1981, Gresswell 1991, Hepworth et al. 2002), including Colorado River cutthroat trout (U.S. Fish and Wildlife Service 2004). Details of how to conduct treatments are described elsewhere (Finlayson et al. 2000, Hepworth et al. 2002), so only a few key points will be addressed here. First, although some projects have involved relatively large stream networks (e.g., 93 km in LaBarge Creek and 78 km in the North Fork Little Snake River; Wyoming

Game and Fish Department 2007), most waters targeted for nonnative fish removal are single streams with low summer discharge (<0.4 m³/s; Hepworth et al. 2002, Brauch and Hebein 2003). Second, these authors noted that in complex streams with numerous side channels, springs, or beaver ponds, single treatments were generally ineffective at removing all nonnative fish. Consequently, toxicants are often applied annually for 2 to 4 years to assure complete removal (Hepworth et al. 2002, Shepard and Nelson 2004, B. Wengert personal communication 2006). In some instances, biologists may notch or remove beaver dams or log jams shortly before chemical application to simplify habitats and increase the efficacy of an individual treatment. Subsequent beaver activity or trapping of debris during high flows often rebuilds these habitats (M.K. Young, personal observation). Although they are relatively successful, chemical applications are increasingly difficult to conduct because of the growing public controversy associated with their use. This may involve concerns about chemicals applied to drinking water supplies (Finlayson et al. 2000) or the loss of valued nonnative trout fisheries (Hepworth et al. 2002). Furthermore, federal policy has been inconsistent with regard to where such treatments will be appropriate, and extended delays in these projects from litigation or administrative review have been commonplace (Finlayson et al. 2005). Often, the costs associated with bureaucratic issues have rendered projects in smaller waters uneconomical (Hepworth et al. 2002).

In part because of these problems, managers have increasingly relied on intensive electrofishing to eliminate nonnative trout from streams in which cutthroat trout will be introduced (Brauch and Hebein 2003, Shepard and Nelson 2004). Initially, attempts to remove nonnative trout often employed a single removal conducted in one or a few years, but this was ineffective because even multiple electrofishing passes over a short period of time do not capture all fish present and small numbers of reproducing adults can quickly repopulate a stream (Thompson and Rahel 1996, Shepard et al. 2002, Meyer et al. 2006a). Successful eradication was associated with more intensive removal efforts (6 to 10, 2-pass removals over 1 to 3 years; Kulp and Moore 2000, Shepard and Nelson 2004). Shepard and Nelson (2004) recommended focusing the first year on reproductive adults, conducting removals twice before spawning and once afterwards (when remaining adults had schooled and juvenile fish had grown enough to be susceptible to this technique), and concentrating the second year on juvenile fish and the few remaining adults. As with chemical treatments, this approach is

generally only effective in small streams (<4 m wide) with simple channels and little overhanging riparian vegetation (Shepard and Nelson 2004).

In circumstances where removal of nonnative trout may be unlikely, partial control of their populations has been promoted as a method to enhance survival of Colorado River cutthroat trout (Thompson and Rahel 1996, Peterson et al. 2004a). Nevertheless, this must be viewed as a temporary measure that will fail unless permanent removal is the ultimate goal, in part because enthusiasm for such projects tends to wane rapidly (Meyer et al. 2006a). For example, annual trap netting and electrofishing removals of brook trout helped promote survival of a population of greenback cutthroat trout in Hidden Valley Creek in Rocky Mountain National Park. With the cessation of these efforts, brook trout rapidly multiplied and greenback cutthroat trout disappeared (B. Rosenlund, U.S. Fish and Wildlife Service, unpublished data). Selective angling targeting brook trout in this stream was also attempted, but harvest was insufficient to affect a decline (U.S. Fish and Wildlife Service 1998; also see Paul et al. 2003). There is also a concern that in mixed species fisheries, anglers will be unable to distinguish between cutthroat trout and the species designated for harvest (Stelfox et al. 2001).

Treatments of mountain lakes have historically relied on toxicants, either applied in late summer and mixed throughout the water column by mechanical means (B. Rosenlund, U.S. Fish and Wildlife Service, unpublished data) or, perhaps most often in lakes without outlets, applied in autumn before or during turnover and allowed to persist overwinter. In some circumstances, intensive gill netting has exterminated nonnative trout populations (Knapp and Matthews 1998). Finally, a more unusual approach was the apparently effective introduction of sterile tiger muskies (*Esox lucius x masquinongy*) to high-elevation Idaho lakes (K. Meyer personal communication 2007; also see Grisak and Marotz 2002), but this has not been thoroughly evaluated. While these actions may be effective in isolated lakes, those with inflows or outflows would additionally require the approaches described above for streams.

Population establishment, maintenance, and salvage: Translocating (or stocking) fish to establish populations is one of the most common tactics employed by biologists. Stockwell and Leberg (2002) noted that about 80 percent of recovery plans for fish listed under the Endangered Species Act called for translocation. These authors addressed a number of issues related to

translocations, as did Williams et al. (1988); some of these are described in more detail below.

Many populations of cutthroat trout have been established from introductions of hatchery stocks (U.S. Fish and Wildlife Service 1998, 2004) and direct transfers of wild fish (Hepworth et al. 2002). Hepworth et al. (2002) noted that direct transfers of 100 to 200 wild fish were adequate to start new cutthroat trout populations in small streams, but that when the objective was to establish a fishery for native trout in larger water bodies (e.g., reservoirs), the much larger numbers of fish afforded by hatchery production were desirable. Typically, most plants of cutthroat trout have consisted of age-0 or age-1 fish (Young et al. 2002). Based on a stage-structured matrix model used to predict population persistence, Hilderbrand (2002) suggested that one-time stocking of a relatively large number of adults (10 percent of potential carrying capacity) was the most successful strategy, but even small introductions spread out over a decade or two increased persistence. Hilderbrand (2002) argued that if individual populations become increasingly isolated in the future and at greater risk of extinction from chance events or inadequate habitat, periodic artificial supplementation (i.e., roughly equivalent to the current practice of mountain-lake stocking where reproduction is unreliable) of Colorado River cutthroat trout may become the norm. However, under these scenarios, it is difficult to envision that artificial selection would be avoided, thus supplementation might be viewed as a last resort for maintenance of a particular population. Alternatively, introducing new individuals to particular populations to avoid inbreeding (i.e., genetic rescue) may hold promise, but this requires substantial knowledge about the genetic status of source and donor populations to avoid eroding the genetic integrity of an existing population (Tallmon et al. 2004).

As noted in the conservation strategy for Colorado River cutthroat trout (CRCT Conservation Team 2006b), new introductions in a basin will generally be of stocks derived from populations indigenous to that basin (although fish of Nanita Lake origin had until recently been stocked statewide for recreational fisheries in high mountain lakes in Colorado; Brauch and Hebein 2003). Yet the tendency for cutthroat trout, including Colorado River cutthroat trout, to show high between-population differentiation (see Genetic structure, above) implies that developing a broodstock representative of a particular basin is a nontrivial exercise because each indigenous population may carry a unique portion of the genome in that basin (cf. Youngson et al. 2003). Moreover, in those cases where indigenous populations

no longer exist, the dilemma becomes whether to introduce fish from an adjacent river basin or use stocks of mixed origin. Aspects of this problem have been explored elsewhere (Krueger et al. 1981; more recently McKay et al. 2005 for plants).

Finally, managers are often adopting the practice of emergency salvage, which involves removing fish from a stream and holding them elsewhere when the loss of a population is perceived as imminent, such as from post-fire flooding or drought (U.S. Fish and Wildlife Service 2004). One of the few published accounts of this approach involves Gila trout that were salvaged (by electrofishing) from a New Mexico stream after a stand-replacing fire but before monsoon rains arrived (Propst et al. 1992). An intense thunderstorm shortly thereafter apparently eliminated all fish from the basin, which was repopulated several years later with descendants of the salvaged fish after the stream channel had begun to stabilize (Brown et al. 2001). Despite this successful example, managers might consider two issues before adopting this tactic: 1) whether salvage is necessary and 2) where and how long fish are to be held. As noted earlier, severe fire is not inevitably followed by debris torrents that might extirpate fish populations, and even those streams experiencing debris torrents rarely suffer complete extirpation of fish populations because native trout readily recolonized from less affected areas up- or downstream (Rieman and Clayton 1997, Sestrich 2005). Alternatively, in the event of extreme drought, cutthroat trout populations may decline dramatically but still persist if refugia such as springs or beaver ponds are present. More problematic might be that drought tends to be a regional rather than local phenomenon, and many populations might be simultaneously threatened. Thus prioritizing salvage efforts and identifying where to put salvaged stocks might best be done long before the need arises. In addition, because of the potential genetic and disease consequences of holding and possibly propagating wild populations outside their native habitat (or even their outright loss from unforeseen accidents such as power failures at hatcheries; also see Unintentional selection, above), detailed planning before conducting salvage appears sensible. Brooks (2006) provides an example of a salvage plan for Gila trout.

Systematic conservation planning: Conservation is expensive and incremental, and we cannot conserve everything (Meir et al. 2004), a point stressed by Quist and Hubert (2004) with respect to cutthroat trout management in the western United States. Societal desires (e.g., the popularity and economic

benefits of fisheries for charismatic nonnative species) and management realities (e.g., removal of nonnative species from large watersheds is not feasible) constrain the number and kind of watersheds available for the protection or restoration of populations of cutthroat trout, a situation typical of that encountered in establishing reserves for terrestrial species (Soulé and Sanjayan 1998, Margules and Pressey 2000). Most reserves for cutthroat trout have probably been created opportunistically as funding, access, and agency cooperation permitted, or they exist by default (e.g., above water diversion structures or natural waterfalls). Such ad hoc approaches to establishing reserves are unlikely to include the waters most suitable for the long-term conservation of cutthroat trout, in part because the waters least prized for other purposes were most likely to be selected (Pressey 1994).

In contrast, systematic reserve planning strives to preserve all existing (or historical) biodiversity and to maintain its persistence or restore it (Margules and Pressey 2000). It explicitly attempts to maximize the chances of representing all biodiversity elements, is transparent and defensible, permits a more efficient allocation of resources and thus a more efficient conservation of biodiversity, and enables the evaluation of unexpected conservation opportunities (Leslie et al. 2003). The prioritization of conservation actions based on systematic conservation planning can help realize conservation goals given limited resources, as well as identify areas where data are needed to make good decisions (Margules and Pressey 2000). Conservation planning for Colorado River cutthroat trout has considered some of the aforementioned points (see Hirsch et al. 2006), but full implementation of this strategy for freshwater fishes has not been attempted (but see Higgins et al. 2005 for a generic model based on habitat and Allendorf et al. 1997 for work on Pacific Northwest salmon).

The elements of a systematic conservation plan have been tailored for individual groups of species, environments, or regions (e.g., Leslie et al. 2003, Roberts et al. 2003), but most follow an outline similar to that developed by Margules and Pressey (2000). These elements can be summarized in five steps.

- 1) Measure and map the units of conservation, which could include populations of a particular size, different life histories, the array of genetic diversity or habitat diversity, some degree of connectivity, or other aspects of individual populations (see below).

- 2) Identify conservation goals, which could include maintaining or establishing specific numbers and locations of populations based on those conservation units.
- 3) Review existing reserves to assess representativeness. In other words, address whether the number and distribution of existing reserves represent all of the important conservation elements.
- 4) Classify potential reserves based on a set of criteria that improves the chances of meeting the goals. These criteria vary greatly among plans but typically include some version of the following two variables. One is irreplaceability, which is the likelihood that a site will be required in a conservation plan to achieve specific targets or its unavailability will disproportionately reduce the options for meeting those targets (Ferrier et al. 2000); restated, it is the proportion of biodiversity within the planning region that would be lost if the site was lost (Meir et al. 2004). Another criterion is cost, which can be measured in a variety of ways. Cost is often viewed as a representation problem, where one attempts to maximize representing all conservation targets in the fewest sites (Cabeza and Moilanen 2001). It also might include the expense of acquiring sites for conservation (such as on private lands), rendering existing sites more suitable (such as by removing nonnative fish), or the political cost of performing an action (such as where anglers are likely to be dissatisfied at the loss of a nonnative trout fishery).
- 5) Select reserves and prioritize for action based on a ranking of these criteria with respect to the original conservation goals. Two of the variables that are usually included at this stage are complementarity and vulnerability. Complementarity is based on the notion that if the site (or population) representing the highest conservation value (whether it be population size, diversity, number of connected populations or size of connected habitat, or some measure of irreplaceability or representativeness) is chosen for a reserve, then the next site (or population) chosen will contain the maximum amount of biodiversity (or greatest value) not already represented

in the first site (Margules and Pressey 2000). Therefore, it reflects information on reserves already chosen and on those not yet selected. The second variable often included in reserve prioritization is vulnerability, which is simply the risk of loss (often of an existing population or the opportunity to conserve it) within a particular period of time. Although prioritization of reserves can be based on simple rankings of value and vulnerability over a limited geographic area (Allendorf et al. 1997), comprehensive assessments of biodiversity (or alternatively, the various forms of diversity represented by a single species such as Colorado River cutthroat trout) may require an approach that is more efficient though computationally intensive (Cabeza and Moilanen 2001, Leslie et al. 2003).

In a systematic conservation plan, the first question to answer might be “what is the unit of conservation?” Within the United States, units of conservation recognized under the Endangered Species Act are evolutionarily significant units or distinct populations segments (Young and Harig 2001). These effectively equivalent terms require that to merit designation, one or more populations must be essentially reproductively isolated and constitute an important component of the evolutionary legacy of the species; this approach prioritizes groups based on existing patterns of variation. Yet Ruckelshaus et al. (2002) cautioned that what needs to be conserved are not only the genetic or ecological novelties that have arisen, but also the capacity for continued evolution (also see Healey and Prince 1995, Waples et al. 2001). Along these lines, Northcote (1992) argued that because environments will undoubtedly continue to change, maintaining the diversity in life history strategies is the best insurance for uncertain times. Ruckelshaus et al. (2002) also suggested that conservation be based to some extent on the recency of evolved traits and the number of times they have arisen. For example, the repeated derivation of resident life histories from migrant ones (Berg 1985, Stearley 1992) implies that this would be a readily “recovered” trait whereas the most complex life histories are probably unique and perhaps unrecoverable if lost. In the absence of data on evolutionary phylogeny of these traits, an alternative is to use the diversity in habitats and associated life histories as the basis for selection of forms to conserve (Northcote 1992, Healey and Prince 1995). Allendorf et al. (1997) suggest other criteria for defining conservation value.

Prioritizing where to work can also be based on other factors. Hepworth et al. (2002) noted there was little opposition to cutthroat trout restoration in small, isolated tributaries, but much less support for work in streams supporting existing fisheries. They suggested prioritizing restoration based on threats and what was attainable. Taking a similar tack in cataloging possible waters for restoration of Colorado River cutthroat trout, Hirsch et al. (2006) considered whether barriers were present or could be built, whether there were records of nonnative fish stocking or reports of nonnative fish present, the feasibility of nonnative fish removal, the condition of existing habitat, and whether there was a popular fishery for nonnative trout. It could be argued that this ranking system tends to favor small, simple (and in some cases, historically barren) streams; although pragmatic from a political and management perspective, such waters would be likely to support relatively small populations susceptible to extirpation and in need of frequent management intervention. A ranking scheme that also favored restoration in streams potentially supporting more robust populations that were resilient to stochastic variation, because they provided greater amounts of habitat or connectivity to additional waters, might suggest some additional priorities for restoration (cf. Feist et al. 2003). Balancing these two perspectives could be a useful element of a prioritization scheme.

On a related note, distinctions are sometimes made between using waters for restoration that were once inhabited by a particular species versus those that were historically barren (Young and Harig 2001). A policy statement from the American Fisheries Society regarded stocking outside historically occupied waters as unacceptable unless formerly occupied habitats were unavailable or unrestorable (Williams et al. 1988). Nevertheless, historically fishless waters have frequently been adopted by agencies charged with recovering rare or threatened taxa, including greenback and Colorado River cutthroat trout (U.S. Fish and Wildlife Service 1998, CRCT Task Force 2001). For example, inaccessible high-elevation lakes have been widely used for introductions because they serve as more stable environs unlikely to lose stocked populations except from winterkill or lack of reproduction. Likewise, many headwater stream segments above waterfalls are fishless, and may be deemed the most suitable sites for introductions for that reason (Hirsch et al. 2006; see above). At least three issues, all noted earlier, deserve consideration with respect to these uses of historically fishless waters. First, introductions there may harm other indigenous species (Dunham et al. 2004). Second, absence of fish from such reaches may indicate that they are unsuitable trout habitat. Harig and Fausch (2002)

and Young et al. (2005) suggested that mean summer water temperature and occupiable stream length could be used as screens to select suitable habitats. Finally, establishing populations in such habitats exposes them to strong natural selection, which probably has little effect in the short term but has long-term implications for maintaining the genetic variability that was exhibited historically. Nonetheless, use of such waters may be unavoidable if climate change and human uses render habitats within the historical range unsuitable.

Information Needs

Many gaps in our understanding of the evolution and ecology of Colorado River cutthroat trout have been identified throughout this paper, but a few warrant further development because they may address crucial short-term issues. One of the most critical needs among biologists working on conservation of native cutthroat trout of all subspecies is a clearinghouse of information on efforts, techniques, and strategies. Syntheses such as this one are a useful start, but more precious, partly because of their rarity, are summaries by practitioners of what worked and what did not (e.g., Hepworth 2002). The websites on barrier construction (<http://wildfish.montana.edu/projects/barrier/browse.asp>) and stream restoration (see Jenkinson et al. 2006) also serve as examples. More controversial but perhaps no less important is greater availability of population size and trend data for many rare and threatened species (in this regard the status assessment [Hirsch et al. 2006] is an excellent start). Availability of this information would invite public participation and independent evaluation of population and species management, which might be uncomfortable for agencies used to controlling access to such data, but which could also lead to more successful management and less controversy over management decisions because of greater public involvement (Safford 1995, James 1999). Dedicated databases are also associated with more cost-efficient and successful conservation (Lundquist et al. 2002).

To date, Hirsch et al. (2006) have compiled the most comprehensive assessment of the status and distribution of existing populations of Colorado River cutthroat trout. They also acknowledged that the description of many population characteristics was based on professional judgment rather than field inventories. For example, they delimited the historical range of Colorado River cutthroat trout by relying on opinions of biologists familiar with the different portions of its range (Hirsch et al. 2006). Where deemed appropriate, this work could be further informed by examination of local historical documents, as has been

done to identify the pre-dam distribution of salmonids in the Klamath River basin (Hamilton et al. 2005), to locate the historical southern limit of coho salmon in California (Kaczynski and Alvarado 2006), and to identify the periods and locations of railroad tie drives in southeastern Wyoming (Young et al. 1994). In addition, whereas it is likely that most populations of Colorado River cutthroat trout have been located, comprehensive inventories of the spatial characteristics of most of these populations – their upstream and downstream extent and the presence of natural or anthropogenic barriers that structure otherwise connected populations (Wofford et al. 2005, Cole et al. 2006; Fransen et al. 2006, Pritchard et al. 2007b) – probably remain incomplete. This was the case for many populations of greenback cutthroat trout, despite the management attention directed at the comparatively few populations of this federally listed taxon (Young and Guenther-Gloss 2004). Such surveys would permit refined estimates of population size and barrier permanence. Moreover, the identification of existing or potential barriers would have implications for the management of Colorado River cutthroat trout populations in a changing climate.

Fundamental to modeling or managing Colorado River cutthroat trout populations is the ability to define them (cf. Dunham et al. 2001). Though apparently intuitive, identifying geographic boundaries of cutthroat trout populations is complicated by the presence of individuals that migrate or stray, by the intermittent suitability of some habitats, and by the continuity of connectivity to or isolation from other waters. Techniques for assessing the genetic distance among individuals or defining genetic neighborhoods (Neville et al. 2006b), stable isotope analyses that permit identification of natal streams of migratory fish (Rieman et al. 1994), and traditional demographic and movement studies will be necessary to understand whether a body of water contains one or more viable populations, represents a demographic sink for surplus fish produced elsewhere, or provides complementary habitat for a population ranging over a much longer stream network. In waters permitting substantial connectivity, autocorrelation in phenotypic or genotypic character sets has been used to define geographic population structure (Diniz-Filho and Telles 2002). In addition, populations have been geographically defined based on their homing to particular spawning locations (Dunham et al. 2001), whether they are within a single stream or distributed among different streams in a network. Alternatively, the entire home range of a group of fishes (Danancher et al. 2004) could serve the same purpose. Although it has been expedient to associate individual Colorado River cutthroat trout populations with a named body of

water (e.g., Young et al. 1996), this has little *a priori* justification unless known barriers confine individuals to a lake or a headwater stream segment. Individuals found below such barriers may represent migrants that are lost from the upstream population, constitute a separate population with a similar or entirely different migration strategy, or both. In addition, as noted earlier, multiple barriers within particular streams may produce semi-independent populations linked by one-way migrations (i.e., under most circumstances, individuals can only move downstream) that may exhibit very different dynamics than single populations occupying a connected patch of similar size. Hirsch et al. (2006) recognized this dilemma and offered what should be regarded as hypotheses about where Colorado River cutthroat trout in different waters may be demographically connected. Studies of fish movement and genetic population structure, coupled with the aforementioned stream inventories, will be necessary to address this issue.

Although genetic approaches have proven to be reliable at detecting hybridization, they remain costly, and managers continue to explore the use of visual techniques for preliminary evaluations (e.g., as a screen for determining whether populations warrant genetic testing). Some of these methods have been at least partly successful. De Rito (2004) was fairly accurate in detecting pure Yellowstone cutthroat trout while recognition of pure rainbow trout and of hybrid individuals was unreliable (also see Campbell et al. 2002, Meyer et al. 2006b). Similar results were obtained with classifications of coastal cutthroat trout, steelhead, and their hybrids (Baumsteiger et al. 2005). More promising was a relatively robust classification tree model for discriminating westslope cutthroat trout from their hybrids with rainbow trout based on the prominence of the throat slashes, basibranchial teeth presence, spot shape, and relative head length (Weigel et al. 2002). Constructing comparable models for Colorado River cutthroat trout would require extensive sampling coupled with genetic assessment of individuals, but collection of individuals for genetic testing may already be planned, and structured visual assessments might be added in the field with little additional effort (e.g., 2 minutes per fish; Weigel et al. 2002).

As noted earlier, extensive sampling has been done to evaluate the genetic purity of many populations of Colorado River cutthroat trout (Hirsch et al. 2006). Beyond the question of purity, however, is the phylogeography and genetic population structure of these populations. As pointed out earlier in this assessment, Colorado River cutthroat trout

may represent an archaic form more closely related to Bonneville cutthroat trout, Rio Grande cutthroat trout, and greenback cutthroat trout, and a modern form influenced by Yellowstone cutthroat trout, but the spatial distribution of these forms (or further evidence of whether they actually exist) is poorly described. Conserving the genetic diversity represented by both of these lineages may be of concern to managers, and management not cognizant of these potentially separate lineages puts them at risk (cf. Bardakci et al. 2006, Sanz et al. 2006). In addition, the stocking of Colorado River cutthroat trout from Trapper's Lake, Colorado was widespread in that state (Young et al. 1996), as was stocking with fish from other locations (Emerald Lake in Hinsdale County and the Grand Mesa lakes in Mesa County, Colorado; Wiltzius 1985). Further genetic assessments may reveal the proportion of current populations that represent anthropogenic introductions of these stocks or those of greenback cutthroat trout or Rio Grande cutthroat trout. Relating measures of

genetic diversity within populations to fitness may also help to elucidate whether inbreeding depression represents a substantial threat.

Because nonnative trout, particularly brook trout, likely represent the greatest current threat to the persistence of many populations of Colorado River cutthroat trout, evaluations of many aspects of these invasions may be crucial. For example, knowledge about the typical rate of advance and demographic establishment of invading fish would give managers some notion of the amount of time they may have to respond before a population of cutthroat trout may be beyond saving. Furthermore, despite their widespread success, brook trout invasions do not appear to be inevitable in all waters, and the environmental characteristics that inhibit those invasions could suggest management approaches for reducing or eliminating brook trout elsewhere, or identify relative levels of risk of particular waters to invasion by brook trout.

DEFINITIONS

Adfluvial – a life history form that uses lakes for rearing and growth but migrates to streams to spawn.

Allopatric – not overlapping in distribution with another species.

Anadromous – a life history form that uses the ocean for rearing and growth but migrates to streams to spawn.

Anchor ice – submerged ice that is attached to the stream bottom. When dislodged or floating in the water column, often referred to as frazil ice.

Anthropogenic – of human origin.

Burst speed – the maximum speed of swimming.

Carotenoid – a reddish pigment.

Caudal peduncle – the tapering portion of a fish's body between the posterior edge of the anal fin base and the base of the caudal fin.

Debris torrent – a flood consisting of water, sediment, rock, and wood that can result when short-duration, high-intensity rainfall exceeds soil infiltration capacity and leads to channeling of surface runoff; such floods usually originate in small, steep basins and often consist of much more than 50 percent sediment, rock, and wood, in contrast to hyperconcentrated flows (sometimes known as blackwater events) that consist of less than 50 percent of these particles.

Deme – a local population that is largely isolated from other populations of the same species.

Deterministic – referring to events that have no random or probabilistic aspects but proceed in a fixed predictable fashion.

Diel – over a 24-h period.

Diurnal – during the day.

Effective population size – the number of adults in an idealized population e.g., with an equal sex ratio and equal contributions among individuals, that would have the same temporal variation in gene frequencies as a population in question.

Extinction – loss of a taxon from all of its range. Often also used to refer to the loss of a population (thus synonymous with extirpation), which is probably appropriate for cutthroat trout because of their local population structuring.

Extirpation – loss of a taxon from part of its range.

Fluvial – a life history form that migrates from rivers or larger streams to small streams to spawn; it also means of rivers or streams (as opposed to lacustrine).

Genetic drift – a random change in the frequencies of alleles that is often inversely proportional to population size and connectivity. Drift frequently leads to loss of alleles and reductions in genetic variability.

Genome – the total genetic material of an individual or species.

Glacial maximum – furthest southward and downward extent of glaciers.

Haplotype – one of the alternative forms of the genotype of a gene complex.

Heterozygosity – having two or more alleles at a particular locus; may apply to an individual or a population.

Homing – Returning to reproduce in the same location where born (in contrast to straying).

Hybridization – production of offspring from mating of separate taxa.

Hybrid swarm – a complete admixture of genetic material from separate taxa within a single population.

Indigenous population – a population native to a water body; this does not include populations in the Colorado River basin that were stocked into historically unoccupied waters, regardless of their hydrologic connection.

Introgression – movement of genetic material from one taxon to another; introgressive hybridization results from production of fertile hybrid offspring that mate with other hybridized or pure individuals.

Isostatic rebound – in this case, land-level rise following the loss of glacial ice; the earth's crust is buoyant, floating on the hot mantle, and removal of water, ice, or sediment from the earth's surface enables those portions to rise, often differentially along fault lines.

Lateral line – a fish organ that runs horizontally under the skin along the sides of a fish.

Macroinvertebrates – with respect to fish, usually invertebrates (e.g., insects, spiders, or annelids) that are large enough to constitute part of the diet.

Migration – directed, often long-distance movements by fish as an element of their life history.

Parr marks – oval, vertically oriented markings on the sides of many salmonids, particularly juveniles.

Piscivory – consuming fish as part of the diet.

Refugia – typically, habitat sanctuaries from extreme environmental events.

Resident – a life history form that confines its migrations to small- to medium-sized streams; the distinction between this and a fluvial life history is somewhat arbitrary and may depend more on the presence of a known barrier restricting the former; sometimes collectively referring to all freshwater life histories in contrast to anadromy.

Salmonid – a member of the family Salmonidae, including trout, charr, salmon, grayling, and whitefish.

Springbrook – a channel in alluvium fed by groundwater that is often adjacent to a larger river.

Stochastic – random.

Stream capture – The redirection of flows from one basin to an adjacent basin, typically by ice or erosion; often responsible for interbasin transfer of fish populations during post- and pre-glacial times.

Sympatric – co-occurring with a particular species.

Vital rates – demographic characteristics (e.g., fecundity and age-specific survival) that determine population growth rate.

REFERENCES

- Adams, C.E. and F.A. Huntingford. 2004. Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. *Biological Journal of the Linnean Society* 81:611-618.
- Adams, S.B. 1999. Mechanisms limiting a vertebrate invasion: brook trout in mountain streams of the northwestern USA. Doctoral dissertation, University of Montana, Missoula, MT.
- Adams, S.B., C.A. Frissell, and B.E. Rieman. 2001. Geography of invasion in mountain streams: consequences of headwater lake fish introductions. *Ecosystems* 2001:296-307.
- Agouridis, C.T., S.R. Workman, R.C. Warner, and G.D. Jennings. 2005. Livestock grazing management impacts on stream water quality: a review. *Journal of the American Water Resources Association* 41:591-606.
- Albanese, B., P.L. Angermeier, and C. Gowan. 2003. Designing mark-recapture studies to reduce effects of distance weighting on movement distance distributions of stream fishes. *Transactions of the American Fisheries Society* 132:925-939.
- Allan, C. and A. Curtis. 2005. Nipped in the bud: why regional scale adaptive management is not blooming. *Environmental Management* 36:414-425.
- Allan, J.D., M.S. Wipfli, J.P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on terrestrial invertebrate subsidies to salmonid food webs. *Canadian Journal of Fisheries and Aquatic Sciences* 60:309-320.
- Allendorf, F.W. and nine others. 1997. Prioritizing Pacific salmon stocks for conservation. *Conservation Biology* 11: 140-152.
- Allendorf, F.W. and R.F. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. *Conservation Biology* 2:170-184.
- Allendorf, F.W., R.F. Leary, N.P. Hitt, K.L. Knudsen, M.C. Boyer, and P. Spruell. 2005. Cutthroat trout hybridization and the U.S. Endangered Species Act: one species, two policies. *Conservation Biology* 19:1326-1328.
- Allendorf, F.W., R.F. Leary, N.P. Hitt, K.L. Knudsen, L.L. Lundquist, and P. Spruell. 2004. Intercrosses and the U.S. Endangered Species Act: should hybridized populations be included as westslope cutthroat trout? *Conservation Biology* 18:1203-1213.
- Allendorf, F.W., R.F. Leary, P. Spruell, and J.K. Wenburg. 2001. The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution* 16:613-620.
- Allendorf, F.W. and N. Ryman. 2002. The role of genetics in population viability analysis. Pages 50-85 *in* S.R. Beissinger and D.R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, IL.
- Amiro, P.G. 1990a. Variation in juvenile Atlantic salmon population densities between consecutive enclosed sections of streams. Pages 96-101 *in* I.G. Cowx, editor. *Developments in electric fishing*. Fishing News Books, Oxford.
- Amiro, P.G. 1990b. Accuracy of removal population estimates of juvenile Atlantic salmon electric fished in wadeable streams. Pages 186-190 *in* I.G. Cowx, editor. *Developments in electric fishing*. Fishing News Books, Oxford.
- Andrewartha, H.G. and L.C. Birch. 1984. *The ecological web: more on the distribution and abundance of animals*. University of Chicago Press, Chicago, IL.
- Angermeier, P.L., K.L. Krueger, and C.A. Dolloff. 2002. Discontinuity in stream-fish assemblages: implications for assessing and predicting species occurrence. Pages 519-527 *in* J.M. Scott, P.J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall. *Predicting species occurrences: issues of scale and accuracy*. Island Press, Covelo, CA.
- Apache Trout/Little Colorado River Spinedace Recovery Team. 2000. Apache trout recovery implementation plan. Pinetop, AZ.

- Araguas, R.M., N. Sanz, C. Pla, and J.L. Garcia-Mari. 2004. Breakdown of the brown trout evolutionary history due to hybridization between native and cultivated fish. *Journal of Fish Biology* 65(Supplement A):28-37.
- Archer, E.K., B.B. Roper, R.C. Henderson, N. Bouwes, S.C. Mellison, and J.L. Kershner. 2004. Testing common stream sampling methods for broad-scale, long-term monitoring. U.S. Forest Service General Technical Report RMRS-GTR-122.
- Avenetti, L.D., A.T. Robinson, and C.J. Cantrell. 2006. Short-term effectiveness of constructed barriers at protecting Apache trout. *North American Journal of Fisheries Management* 26:213-216.
- Bahls, P. 1992. The status of fish populations and management of high mountain lakes in the western United States. *Northwest Science* 66:183-193.
- Bain, M.B. and N.J. Stevenson, editors. 1999. *Aquatic habitat assessment: common methods*. American Fisheries Society, Bethesda, MD.
- Baldwin, C.M., D.A. Beauchamp, and J.J. Van Tassell. 2000. Bioenergetic assessment of temporal food supply and consumption demand by salmonids in the Strawberry Reservoir food web. *Transactions of the American Fisheries Society* 129:429-450.
- Bardakci, F., N. Degerli, O. Ozdemir, and H.H. Basibuyuk. 2006. Phylogeography of the Turkish brown trout *Salmo trutta* L.: mitochondrial DNA PCRRFLP variation. *Journal of Fish Biology* 68:36-55.
- Bart, J., K.P. Burnham, E.H. Dunn, C.M. Francis, and C.J. Ralph. 2004. Goals and strategies for estimating trends in landbird abundance. *Journal of Wildlife Management* 68:611-626.
- Barton, B.A. and W.P. Dwyer. 1997. Physiological stress effects of continuous- and pulsed-DC electroshock on juvenile bull trout. *Journal of Fish Biology* 51:998-1008.
- Bash, J.S. and C.M. Ryan. 2002. Stream restoration and enhancement projects: is anyone monitoring? *Environmental Management* 29:877-885.
- Bateman, D.S., R.E. Gresswell, and C.E. Torgersen. 2005. Evaluating single-pass catch as a tool for identifying spatial pattern in fish distribution. *Journal of Freshwater Ecology* 20:335-345.
- Baumsteiger, J., D. Hankin, and E.J. Loudenslager. 2005. Genetic analyses of juvenile steelhead, coastal cutthroat trout, and their hybrids differ substantially from field identifications. *Transactions of the American Fisheries Society* 134:829-840.
- Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201-220.
- Baxter, G.T. and M.D. Stone. 1995. *Fishes of Wyoming*. Wyoming Game and Fish Department, Cheyenne.
- Bear, B.E. 2005. Effects of temperature on survival and growth of westslope cutthroat trout and rainbow trout: implications for conservation and restoration. Master's thesis, Montana State University, Bozeman, Montana.
- Beauchamp, K.A. and six others. 2002. Prevalence and susceptibility of infection to *Myxobolus cerebralis*, and genetic differences among populations of *Tubifex tubifex*. *Diseases of Aquatic Organisms* 51:113-121.
- Beaumont, W.R.C., M.J. Lee, and G. Peirson. 2005. The equivalent resistance and power requirements of electric fishing electrodes. *Fisheries Management and Ecology* 12:37-43.
- Beaumont, W.R.C., G. Peirson, and M.J. Lee. 2006. Factors affecting the characteristics and propagation of voltage gradient fields from electric fishing electrodes. *Fisheries Management and Ecology* 13:47-52.
- Beechie, T. and S. Bolton. 1999. An approach to restoring salmonid habitat-forming processes in Pacific Northwest watersheds. *Fisheries* 24(4):6-15.
- Behnke, R.J. 1979. Monograph of the native trouts of the genus *Salmo* of western North America. USDA Forest Service, Rocky Mountain Region, Denver, CO.
- Behnke, R.J. 1992. Native trout of western North America. American Fisheries Society Monograph 6.

- Behnke, R.J. and D.E. Benson. 1980. Endangered and threatened fish of the upper Colorado River basin. Bulletin 503A. Cooperative Extension Service, Colorado State University, Fort Collins, CO.
- Behnke, R.J. and M. Zarn. 1976. Biology and management of threatened and endangered western trout. USDA Forest Service General Technical Report RM-28.
- Beissinger, S.R. and D.R. McCullough, editors. 2002. Population viability analysis. University of Chicago Press, Chicago, IL.
- Beissinger, S.R. and M.I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821-841.
- Belsky, A.J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. *Journal of Soil and Water Conservation* 54:419-431.
- Benda, L.E., D.J. Miller, T. Dunne, G.H. Reeves, and J.K. Agee. 1998. Dynamic landscape systems. Pages 261-288 in R.J. Naiman and R.E. Bilby, editors. *River ecology and management: lessons from the Pacific Coastal ecoregion*. Springer-Verlag, NY.
- Benjamin, J.R., J.B. Dunham, and M.R. Dare. 2007. Invasion by nonnative brook trout in Panther Creek, Idaho: roles of local habitat quality, biotic resistance, and connectivity to source habitats. *Transactions of the American Fisheries Society* 136:875-888.
- Benson, L., R. Madole, G. Landis, and J. Gosse. 2005. New data for Late Pleistocene Pinedale alpine glaciation from southwestern Colorado. *Quaternary Sciences Reviews* 24:49-65.
- Benson, N.G. 1960. Factors influencing production of immature cutthroat trout in Arnica Creek, Yellowstone Park. *Transactions of the American Fisheries Society* 89:168-175.
- Berg, O.K. 1985. The formation of non-anadromous population of Atlantic salmon in Europe. *Journal of Fish Biology* 27:805-815.
- Bergersen, E.P. and D.E. Anderson. 1997. The distribution and spread of *Myxobolus cerebralis* in the United States. *Fisheries* 22(8):6-7.
- Bernard, D.R. and E.K. Israelsen. 1982. Inter- and intrastream migration of cutthroat trout (*Salmo clarki*) in Spawn Creek, a tributary of the Logan River, Utah. *Northwest Science* 56:148-158.
- Bernhardt, E.S. and 24 others. 2005. Synthesizing U.S. river restoration efforts. *Science* 28:636-637.
- Beschta, R.L. and eight others. 2004. Postfire management on forested public lands of the western United States. *Conservation Biology* 18:957-967.
- Binns, N.A. 1977. Present status of indigenous populations of cutthroat trout, *Salmo clarki*, in southwest Wyoming. *Fisheries Technical Bulletin* 2. Wyoming Game and Fish Department, Cheyenne, WY.
- Binns, N.A. 2004. Effectiveness of habitat manipulation for wild salmonids in Wyoming streams. *North American Journal of Fisheries Management* 24:911-921.
- Bisbal, G.A. 2001. Conceptual design of monitoring and evaluation plans for fish and wildlife in the Columbia River ecosystem. *Environmental Management* 28:433-453.
- Bischoff, C.M. 1995. Introgression between Colorado River cutthroat trout and rainbow trout in an isolated drainage system. Master's thesis, Utah State University, Logan, UT.
- Bisson, P.A., S.M. Wondzell, G.H. Reeves, and S.V. Gregory. 2003. Trends in using wood to restore aquatic habitats and fish communities in western North American rivers. *American Fisheries Society Symposium* 37:391-406.
- Bjornn, T.C. and J. Mallet. 1964. Movements of planted and wild trout in an Idaho river system. *Transactions of the American Fisheries Society* 93:70-76.
- Bohlin, T. 1982. The validity of removal method for small populations-consequences for electrofishing practice. Report of the Institute of Freshwater Research Drottningholm 60:15-18.

- Bohlin, T. and B. Sundström. 1977. Influence of unequal catchability on population estimates using the Lincoln index and the removal method applied to electro-fishing. *Oikos* 28:123-129.
- Bohlin, T., S. Hamrin, T.G. Heggberget, G. Rasmussen, and S.J. Saltveit. 1989. Electrofishing-theory and practice with special emphasis on salmonids. *Hydrobiologia* 173:9-43.
- Bond, N.R. and P.S. Lake. 2003. Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. *Ecological Management & Restoration* 4:193-198.
- Bonneau, J.L. and D.L. Scarnecchia. 1998. Seasonal and diel changes in habitat use by juvenile bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) in a mountain stream. *Canadian Journal of Zoology* 76: 783-790.
- Borgström, R. and J. Museth. 2005. Accumulated snow and summer temperature—critical factors for recruitment to high mountain populations of brown trout (*Salmo trutta* L.). *Ecology of Freshwater Fish* 14:375-384.
- Bormann, B.T., R.W. Haynes, and J.R. Martin. 2007. Adaptive management of forest ecosystems: did some rubber hit the road? *BioScience* 57:186-191.
- Boss, S.M. and J.S. Richardson. 2002. Effects of food and cover on the growth, survival, and movement of cutthroat trout (*Oncorhynchus clarki*) in coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1044-1053.
- Bowman, W.D., D.M. Cairns, J.S. Baron, and T.R. Seastedt. 2002. Islands in the sky: tundra and treeline ecosystems of the Rockies. Pages 183-202 in J.S. Baron, editor. *Rocky Mountain futures: an ecological perspective*. Island Press, Washington, D.C.
- Bozek, M.A. and W.A. Hubert. 1992. Segregation of resident trout in streams as predicted by three habitat dimensions. *Canadian Journal of Zoology* 70:886-890.
- Bozek, M.A. and F.J. Rahel. 1991a. Comparison of streamside visual counts to electrofishing estimates of Colorado River cutthroat trout fry and adults. *North American Journal of Fisheries Management* 11:38-42.
- Bozek, M.A. and F.J. Rahel. 1991b. Assessing habitat requirements of young Colorado River cutthroat trout by use of macrohabitat and microhabitat analyses. *Transactions of the American Fisheries Society* 120:571-581.
- Bozek, M.A. and M.K. Young. 1994. Fish mortality resulting from delayed effects of fire in the Greater Yellowstone Ecosystem. *Great Basin Naturalist* 54:91-95.
- Bozek, M.A., L.D. DeBrey, and J.A. Lockwood. 1994. Diet overlap among size classes of Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in a high-elevation mountain stream. *Hydrobiologia* 273:9-17.
- Braennaes, E. H. Lundqvist, E. Prentice, M. Schmitz, K. Braennaes, and B.-S. Wiklund. 1994. Use of the passive integrated transponder (PIT) in a fish identification and monitoring system for fish behavioral studies. *Transactions of the American Fisheries Society* 123:395-401.
- Bragg, D.C. 2000. Simulating catastrophic and individualistic large woody debris recruitment for a small riparian system. *Ecology* 81:1383-1394.
- Bragg, D.C., J.L. Kershner, and D.W. Roberts. 2000. Modeling large woody debris recruitment for small streams of the central Rocky Mountains. U.S. Forest Service General Technical Report RMRS-GTR-55.
- Brannon, E.L. and 10 others. 2004. The controversy about salmon hatcheries. *Fisheries* 29(9):12-31.
- Brauch, D.E. and S. Hebein. 2003. Colorado River cutthroat trout management in western Colorado during 1999-2002. Colorado Division of Wildlife, Denver, CO.
- Brook, B.W., M.A. Burgman, H.R. Akcakaya, J.J. O'Grady, and R. Frankham. 2002. Critiques of PVA ask the wrong questions: throwing the heuristic baby out with the numerical bath water. *Conservation Biology* 16:262-263.
- Brook, B.W., J.J. O'Grady, A.P. Chapman, M.A. Burgman, H.R. Akcakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404:385-387.

- Brooks, J. 2006. Emergency evacuation procedures for Gila trout. U.S. Fish and Wildlife Service, Albuquerque, NM. 16 p.
- Brown, D.K., A.A. Echelle, D.L. Propst, J.E. Brooks, and W.L. Fisher. 2001. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout (*Oncorhynchus gilae*). *Western North American Naturalist* 61:139-148.
- Brown, R.S. 1999. Fall and early winter movements of cutthroat trout, *Oncorhynchus clarki*, in relation to water temperature and ice conditions in Dutch Creek, Alberta. *Environmental Biology of Fishes* 55:359-368.
- Brown, R.S. and W.C. Mackay. 1995a. Spawning ecology of cutthroat trout (*Oncorhynchus clarki*) in the Ram River, Alberta. *Canadian Journal of Fisheries and Aquatic Sciences* 52:983-992.
- Brown, R.S. and W.C. Mackay. 1995b. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. *Transactions of the American Fisheries Society* 124:873-885.
- Bryant, M.D., R.T. Edwards, and R.D. Woodsmith. 2005. An approach to effectiveness monitoring of floodplain channel aquatic habitat:salmonid relationships. *Landscape and Urban Planning* 72:157-176.
- Buffington, J.M., D.R. Montgomery and H.M. Greenberg. 2004. Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments. *Canadian Journal of Fisheries and Aquatic Sciences* 61:2085-2096.
- Bureau of Land Management. 2002. BLM Wyoming sensitive species policy and list. Available online: <http://www.blm.gov/pgdata/etc/medialib/blm/wy/wildlife.Par.9226.File.dat/02species.pdf>.
- Burton, T.A. 2005. Fish and stream habitat risks from uncharacteristic wildfire: observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. *Forest Ecology and Management* 211:140-149.
- Busack, C.A. and G.A.E. Gall. 1981. Introgressive hybridization in populations of Paiute cutthroat trout (*Salmo clarki seleniris*). *Canadian Journal of Fisheries and Aquatic Sciences* 38:939-951.
- Büttiker, B. 1992. Electrofishing results corrected by selectivity functions in stock size estimates of brown trout (*Salmo trutta* L.) in brooks. *Journal of Fish Biology* 41:673-684.
- Cabeza, M. and A. Moilanen. 2001. Design of reserve networks and the persistence of biodiversity. *Trends in Ecology & Evolution* 16:242-248.
- Calamusso, B. and J.N. Rinne. 2004. Distribution and abundance of Rio Grande cutthroat trout (*Oncorhynchus clarki virginalis*), relative to an introduced salmonid, in northern New Mexico. Pages 31-37 in G.J. Scrimgeour, G. Eisler, B. McCulloch, U. Silins, and M. Monita, editors. *Proceedings of the Forest Land—Fish Conference II*, 26-28 April, 2004, Edmonton, Alberta.
- Campbell, M.R., J. Dillon, and M.S. Powell. 2002. Hybridization and introgression in a managed, native population of Yellowstone cutthroat trout: genetic detection and management implications. *Transactions of the American Fisheries Society* 131:364-375.
- Campton, D. 2004. Sperm competition in salmon hatcheries: the need to institutionalize genetically benign spawning protocols. *Transactions of the American Fisheries Society* 133:1277-1289.
- Campton, D. and L.R. Kaeding. 2005. Westslope cutthroat trout, hybridization, and the U.S. Endangered Species Act. *Conservation Biology* 19:1323-1325.
- Cannon, S.H. 1999. Debris-flow response of watersheds recently burned by wildfire. Doctoral dissertation, University of Colorado, Boulder, Colorado.
- Carl, L.M. and J.D. Stelfox. 1989. A meristic, morphometric, and electrophoretic analysis of cutthroat trout *Salmo clarki*, from two mountain lakes in Alberta. *Canadian Field-Naturalist* 103:80-84.
- Carlsson, J. and J. Nilsson. 2001. Effects of geomorphological structures on genetic differentiation among brown trout populations in a northern boreal river drainage. *Transactions of the American Fisheries Society* 130:36-45.

- Caro, T.M. and M.K. Laurenson. 1994. Ecological and genetic factors in conservation: a cautionary tale. *Science* 263: 485-486.
- Castric, V., F. Bonney, and L. Bernatchez. 2001. Landscape structure and hierarchical genetic diversity in the brook charr, *Salvelinus fontinalis*. *Evolution* 55:1016-1028.
- Cegelski, C.C., M.R. Campbell, K.A. Meyer, and M.S. Powell. 2006. Multiscale genetic structure of Yellowstone cutthroat trout in the upper Snake River basin. *Transactions of the American Fisheries Society* 135:711-726.
- Chapman, D.W. 1966. Food and space as regulators of salmonid populations in streams. *American Naturalist* 100: 345-357.
- Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* 117:1-21.
- Chisholm, I.M., W.A. Hubert, and T.A. Wesche. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. *Transactions of the American Fisheries Society* 116:176-184.
- Christensen, J.H., and 16 others. 2007. Regional climate projections. Chapter 11. Pages 847-940 in S.D. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller, editors. *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* Cambridge University Press, NY.
- Clague, J.J. and T.S. James. 2002. History and isostatic effects of the last ice sheet in southern British Columbia. *Quaternary Science Reviews* 21:71-87.
- Clancy, C.G. 1988. Effects of dewatering on spawning by Yellowstone cutthroat trout in tributaries to the Yellowstone River, Montana. *American Fisheries Society Symposium* 4:37-41.
- Clapp, D.F., R.D. Clark, and J.S. Diana. 1990. Range, activity, and habitat of large, free-ranging brown trout in a Michigan stream. *Transactions of the American Fisheries Society* 119:1022-1034.
- Clarkson, R.W. and J.R. Wilson. 1995. Trout biomass and stream habitat relationships in the White Mountains area, east-central Arizona. *Transactions of the American Fisheries Society* 124:599-612.
- Colautti, R.I. 2005. Are characteristics of introduced salmonid fishes biased by propagule pressure? *Canadian Journal of Fisheries and Aquatic Sciences* 62:950-959.
- Cole, M.B., D.M. Price, and B.R. Fransen. 2006. Change in the upper extent of fish distribution in eastern Washington streams between 2001 and 2002. *Transactions of the American Fisheries Society* 135:634-642.
- Coleman, M.A., and K.D. Fausch. 2007a. Cold summer temperature regimes cause a recruitment bottleneck in age-0 Colorado River cutthroat trout reared in a laboratory stream. *Transactions of the American Fisheries Society* 136:639-654.
- Coleman, M.A., and K.D. Fausch. 2007b. Cold summer temperature limits recruitment of age-0 cutthroat trout in high-elevation Colorado streams. *Transactions of the American Fisheries Society* 136:1231-1244.
- Coles-Ritchie, M., R.C. Henderson, E.K. Archer, B.B. Roper, C. Kennedy, and J.L. Kershner. 2004. The repeatability of riparian vegetation sampling methods: how useful are these techniques for broad-scale, long-term monitoring? USDA Forest Service General Technical Report RMRS-GTR-138.
- Collen, P. and R.J. Gibson. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish—a review. *Reviews in Fish Biology and Fisheries* 10:439-461.
- Colyer, W.T., J.L. Kershner, and R.H. Hilderbrand. 2005. Movements of fluvial Bonneville cutthroat trout in the Thomas Fork of the Bear River, Idaho-Wyoming. *North American Journal of Fisheries Management* 25:954-963.

- Consuegra, S., E. Verspoor, D. Knox, and C. García de Leániz. 2005. Asymmetric gene flow and the evolutionary maintenance of genetic diversity in small, peripheral Atlantic salmon populations. *Conservation Genetics* 6: 823-842.
- Cooney, S.J., A.P. Covich, P.M. Lukacs, A.L. Harig, and K.D. Fausch. 2005. Modeling global warming scenarios in greenback cutthroat trout (*Oncorhynchus clarki stomias*) streams: implications for species recovery. *Western North American Naturalist* 65:371-381.
- Coulson, T., G.M. Mace, E. Hudson, and H. Possingham. 2001. The use and abuse of population viability analysis. *Trends in Ecology and Evolution* 16:219-221.
- Cowx, I.G., editor. 1990. *Developments in electric fishing*. Fishing News Books, Oxford.
- Cowx, I.G. and P.A. Frear. 2004. Assessment of year class strength in freshwater recreational fish populations. *Fisheries Management and Ecology* 11:117-123.
- Cowx, I.G. and P. Lamarque, editors. 1990. *Fishing with electricity: applications in freshwater fisheries management*. Fishing News Books, Oxford.
- Cowx, I.G. and M. van Zyll de Jong. 2004. Rehabilitation of freshwater fisheries: tales of the unexpected? *Fisheries Management and Ecology* 11:243-249.
- Cox, G.W. 2004. *Alien species and evolution*. Island Press, Washington, D.C.
- CRCT Conservation Team. 2006a. Conservation agreement for Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) in the states of Colorado, Utah, and Wyoming. Colorado Division of Wildlife, Fort Collins, CO. 10 p.
- CRCT Conservation Team. 2006b. Conservation strategy for Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) in the states of Colorado, Utah, and Wyoming. Colorado Division of Wildlife, Fort Collins, CO. 24 p.
- CRCT Coordination Team. 2005. Colorado River cutthroat (*Oncorhynchus clarkii pleuriticus*) management activities and accomplishment report: 1999-2003 Colorado, Wyoming and Utah. Colorado Division of Wildlife, Fort Collins, CO.
- CRCT Task Force 2001. Conservation agreement and strategy for Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) in the states of Colorado, Utah, and Wyoming. Colorado Division of Wildlife, Fort Collins, CO. 106 p.
- Crisp, D.T. and P.A. Carling. 1989. Observations on siting, dimensions and structure of salmonid redds. *Journal of Fish Biology* 34:119-134.
- Crnokrak, P. and D.A. Roff. 1999. Inbreeding depression in the wild. *Heredity* 83:260-270.
- Cross, D.G. and B. Stott. 1975. The effect of electric fishing on the subsequent capture of fish. *Journal of Fish Biology* 7:349-357.
- Cunjak, R.A. and G. Power. 1987. Cover use by stream-resident trout in winter: a field experiment. *North American Journal of Fisheries Management* 7:539-544.
- Danancher, D., J. Labonne, R. Pradel, and P. Gaudin. 2004. Capture-recapture estimates of space used in streams (CRESUS) at the population scale: case study on *Zingel asper* (percid), a threatened species of the Rhône catchment. *Canadian Journal of Fisheries and Aquatic Sciences* 61:476-486.
- de la Hoz Franco, E. and P. Budy. 2005. Effects of biotic and abiotic factors on the distribution of trout and salmon along a longitudinal stream gradient. *Environmental Biology of Fishes* 72:379-391.
- De Rito, J.N., Jr. 2004. Assessment of reproductive isolation between Yellowstone cutthroat trout and rainbow trout in the Yellowstone River, Montana. Master's thesis, Montana State University, Bozeman, MT.

- De Staso, J. and F.J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. *Transactions of the American Fisheries Society* 123: 289-297.
- Decker, L.M. and D.C. Erman. 1992. Short-term seasonal changes in composition and abundance of fish in Sagehen Creek, California. *Transactions of the American Fisheries Society* 121:297-306.
- Dickerson, B.R. and G.L. Vinyard. 1999. The effects of high chronic temperatures and diel temperature cycles on the survival and growth of Lahontan cutthroat trout. *Transactions of the American Fisheries Society* 128:516-521.
- Diniz-Filho, J.A.F. and M.P.C. Telles. 2002. Spatial autocorrelation analysis and the identification of operational units for conservation in continuous populations. *Conservation Biology* 16:924-935.
- Dolan, C.R. and L.E. Miranda. 2003. Immobilization thresholds of electrofishing relative to fish size. *Transactions of the American Fisheries Society* 132:969-976.
- Dolloff, C., J. Kershner, and R. Thurow. 1996. Underwater observation. Pages 533-554 *in* B.R. Murphy and D.W. Willis, editors. *Fisheries techniques*. 2nd edition. American Fisheries Society, Bethesda, MD.
- Dolloff, C.A. 1986. Effects of stream cleaning on juvenile coho salmon and Dolly Varden in southeast Alaska. *Transactions of the American Fisheries Society* 115:743-755.
- Dolloff, C.A. and J.L. Warren, Jr. 2003. Fish relationships with large wood in small streams. *American Fisheries Society Symposium* 37:179-193.
- Dolloff, C.A., D.G. Hankin, and G.H. Reeves. 1993. Basinwide estimation of habitat and fish populations in streams. USDA Forest Service General Technical Report SE-83.
- Dowling, T.E. and M.R. Childs. 1992. Impact of hybridization in a threatened trout of the southwestern United States. *Conservation Biology* 6:355-364.
- Downing, D.C., T.E. McMahon, B.L. Kerans, and E.R. Vincent. 2002. Relation of spawning and rearing life history of rainbow trout and susceptibility to *Myxobolus cerebralis* infection in the Madison River, Montana. *Journal of Aquatic Animal Health* 14:191-203.
- Downs, C.C., R.G. White, and B.B. Shepard. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. *North American Journal of Fisheries Management* 17:85-92.
- Drummond, R.A. 1966. Reproduction and harvest of cutthroat trout at Trappers Lake, Colorado. Colorado Department of Game, Fish and Parks, Denver. Special Report 10.
- Dunham, J., D.S. Pilliod, and M.K. Young. 2004. Nonnative trout in headwater systems: the costs of a recreational resource. *Fisheries* 29(6):18-26.
- Dunham, J., R. Schroeter, and B. Rieman. 2003a. Influence of maximum water temperature on occurrence of Lahontan cutthroat trout within streams. *North American Journal of Fisheries Management* 23:1042-1049.
- Dunham, J.B. and B.E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. *Ecological Applications* 9:642-655.
- Dunham, J.B. and G.L. Vinyard. 1997. Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1025-1030.
- Dunham, J.B., B.E. Rieman, and J.T. Peterson. 2002b. Patch-based models to predict species occurrence: lessons from salmonid fishes in streams. Pages 327-334 *in* J.M. Scott, P.J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall. *Predicting species occurrences: issues of scale and accuracy*. Island Press, Covelo, California.
- Dunham, J.B., G.L. Vinyard, and B.E. Rieman. 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. *North American Journal of Fisheries Management* 17:1126-1133.

- Dunham, J.B., S.B. Adams, R.E. Schroeter, and D.C. Novinger. 2002a. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and potential impacts on inland cutthroat trout in western North America. *Reviews in Fish Biology and Fisheries* 12:373-391.
- Dunham, J.B., M.E. Rahn, R.E. Schroeter, and S.W. Breck. 2000. Diets of sympatric Lahontan cutthroat trout and nonnative brook trout: implications for species interactions. *Western North American Naturalist* 60:304-310.
- Dunham, J.B., M.K. Young, R.E. Gresswell, and B.E. Rieman. 2003b. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and nonnative fish invasions. *Forest Ecology and Management* 178:183-196.
- Dunham, J.B., M.M. Peacock, B.E. Rieman, R.E. Schroeter, and G.L. Vinyard. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. *Transactions of the American Fisheries Society* 128:875-889.
- Dunnigan, J.L. 1997. The spatial distribution of cutthroat trout in the Coeur d' Alene River system, Idaho. Master's thesis, University of Idaho, Moscow.
- Dunning, J.B., B.J. Danielson, and H.R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169-175.
- Dwyer, W.P. and R.H. Kramer. 1975. The influence of temperature on scope for activity in cutthroat trout, *Salmo clarki*. *Transactions of the American Fisheries Society* 104:552-554.
- Eaglin, G.S. and W.A. Hubert. 1993. Effects of logging and roads on substrate and trout in streams of the Medicine Bow National Forest, Wyoming. *North American Journal of Fisheries Management* 13:844-846.
- Elliott, J.M., M.A. Hurley, and J.A. Elliott. 1997. Variable effects of droughts on the density of sea-trout *Salmo trutta* over 30 years. *Journal of Applied Ecology* 34:1229-1238.
- Ellner, S.P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. *Conservation Biology* 16:258-261.
- Fausch, K.D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? *Physiology and Ecology Japan, Special Volume* 1:303-322.
- Fausch, K.D. and M.K. Young. 2004. Interactions between forests and fish in the Rocky Mountains of the U.S. Pages 463-484 in T. G. Northcote and G. F. Hartman, editors. *Fishes and forestry - worldwide watershed interactions and management*. Blackwell Science, Oxford.
- Fausch, K.D., C.L. Hawkes, and M.G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950-85. *USDA Forest Service General Technical Report PNW-GTR-213*.
- Fausch, K.D., B.E. Rieman, M.K. Young, and J.B. Dunham. 2006. Strategies for conserving native salmonid populations at risk from nonnative fish invasions: tradeoffs in using barriers to upstream movement. *USDA Forest Service General Technical Report RMRS-GTR-174*.
- Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *BioScience* 52:483-498.
- Fausch, K.D., Y. Taniguchi, S. Nakano, G.D. Grossman, and C.R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecological Applications* 11:1438-1455.
- Fefferman, N.H. and J.M. Reed. 2006. A vital rate sensitivity analysis for nonstable age distributions and short-term planning. *Journal of Wildlife Management* 70:649-656.
- Feist, B.E., E.A. Steel, G.R. Pess, and R.E. Bilby. 2003. The influence of scale on salmon habitat restoration priorities. *Animal Conservation* 6:271-282.
- Ferrier, S., R.L. Pressey, and T.W. Barrett. 2000. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. *Biological Conservation* 93:303-325.

- Ficke, A., P. Guenther-Gloss, and K. Sexton. 2003. Status and trend of native cutthroat trout habitat and populations on the Arapaho and Roosevelt National Forests, Colorado. Arapaho-Roosevelt National Forest, Fort Collins, CO.
- Finlayson, B. and 11 others. 2005. Native inland trout restoration on national forests in the western United States: time for improvement? *Fisheries* 30(5):10-19.
- Finlayson, B.J. and seven others. 2000. Rotenone use in fisheries management: administrative and technical guidelines. American Fisheries Society, Bethesda, MD.
- Fitzpatrick, F.A., I.R. Waite, P.J. D'Arconte, M.R. Meador, M.A. Maupin, and M.E. Gurtz. 1998. Revised methods for characterizing stream habitat in the National Water-Quality Assessment Program. U.S. Geological Survey, Water-Resources Investigations Report 98-4052.
- Flagg, T.A., C.V.W. Mahnken, and R.N. Iwamoto. 2004. Conservation hatchery protocols for Pacific salmon. *American Fisheries Society Symposium* 44:603-619.
- Flebbe, P.A., L.D. Roghair, and J.L. Bruggink. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. *Transactions of the American Fisheries Society* 135:1371-1382.
- Forbes, S.H. and F.W. Allendorf. 1991. Mitochondrial genotypes have no detectable effects on meristic traits in cutthroat trout hybrid swarms. *Evolution* 45:1350-1359.
- Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology* 16:815-825.
- Ford, M.J. 2004. Conservation units and conserving diversity. Pages 338-357 in A.P. Hendry and S.C. Stearns, editors. *Evolution illuminated: salmon and their relatives*. Oxford University Press, NY.
- Fraleigh, J. and B.B. Shepard. 2005. Age, growth, and movements of westslope cutthroat trout, *Oncorhynchus clarki lewisi*, inhabiting the headwaters of a wilderness river. *Northwest Science* 79:12-21.
- Franco, A.M.A. and seven others. 2006. Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biology* 12:1545-1553.
- Frankham, R. 2005. Genetics and extinction. *Biological Conservation* 126:131-140.
- Fransen, B.R., S.D. Duke, L.G. McWethy, J.K. Walter, and R.E. Bilby. 2006. A logistic regression model for predicting the upstream extent of fish occurrence based on geographical information systems data. *North American Journal of Fisheries Management* 26:960-975.
- Frissell, C.A. and R.K. Nawa. 1992. Incidence and causes of physical failure of artificial habitat structures in streams of western Oregon and Washington. *North American Journal of Fisheries Management* 12:182-197.
- Funk, J.L. 1957. Movement of stream fishes in Missouri. *Transactions of the American Fisheries Society* 85:39-57.
- Ganio, L.M., C.E. Torgersen, and R.E. Gresswell. 2005. A geostatistical approach for describing spatial pattern in stream networks. *Frontiers in Ecology and the Environment* 3:138-144.
- Gardiner, W.R. 1984. Estimating population densities of salmonids in deep water in streams. *Journal of Fish Biology* 24:41-49.
- Gatz, A.J., Jr. and J.M. Loar. 1988. Petersen and removal population size estimates: combining methods to adjust and interpret results when assumptions are violated. *Environmental Biology of Fishes* 21:293-307.
- Gerking, S.D. 1959. The restricted movement of fish populations. *Biological Review* 34:221-242.
- Gilbert, M.A. and W.O. Granath, Jr. 2003. Whirling disease of salmonid fish: life cycle, biology, and disease. *Journal of Parasitology* 89:658-667.
- Gislason, D., M.M. Ferguson, S. Skúlason, and S.S. Snorrason. 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences* 56:2229-2234.

- Goodman, D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. *Canadian Journal of Fisheries and Aquatic Sciences* 62:374-389.
- Gowan, C. 2007. Short-term cues used by foraging trout in a California stream. *Environmental Biology of Fishes* 78: 317-331.
- Gowan, C. and K.D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1370-1381.
- Gowan, C. and K.D. Fausch. 2002. Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes* 64:139-153.
- Gowan, C., M.K. Young, K.D. Fausch, and S.C. Riley. 1994. The restricted movement of stream-resident salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences* 51:2626-2637.
- Graves, G.R. 2001. Factors governing the distribution of Swainson's Warbler along a hydrological gradient in Great Dismal Swamp. *The Auk* 118:650-664.
- Gregory, S.V., M.A. Meleason, and D.J. Sobota. 2003. Modeling the dynamics of wood in streams and rivers. *American Fisheries Society Symposium* 37:315-335.
- Gresswell, R.E. 1991. Use of antimycin for removal of brook trout from a tributary of Yellowstone Lake. *North American Journal of Fisheries Management* 11:83-90.
- Gresswell, R.E. 1995. Yellowstone cutthroat trout. Pages 36-54 in M.K. Young, technical editor. Conservation assessment for inland cutthroat trout. USDA Forest Service General Technical Report RM-GTR-256.
- Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* 128:193-221.
- Gresswell, R.E., W.J. Liss, and G.L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. *Canadian Journal of Fisheries and Aquatic Sciences* 51 (Supplement 1):298-309.
- Gresswell, R.E., W.J. Liss, G.L. Larson, and P.J. Bartlein. 1997. Influence of basin-scale physical variables on life history characteristics of cutthroat trout in Yellowstone Lake. *North American Journal of Fisheries Management* 17:1046-1064.
- Griffith, J.S. 1988. Review of competition between cutthroat trout and other salmonids. *American Fisheries Society Symposium* 4:1173-1185.
- Grisak, G. and B. Marotz. 2002. South Fork Flathead Watershed westslope cutthroat trout conservation program. Bonneville Power Administration, Portland, Oregon. Project No. 1991-01903. BPA Report DOE/BP-00005043-1.
- Habera, J.W., R.J. Strange, and S.E. Moore. 1992. Stream morphology affects trout capture efficiency of an AC backpack electrofisher. *Journal of the Tennessee Academy of Science* 67:55-58.
- Hakala, J.P. and K.J. Hartman. 2004. Drought effect on stream morphology and brook trout (*Salvelinus fontinalis*) populations in forested headwater streams. *Hydrobiologia* 515:203-213.
- Ham, K.D. and T.N. Pearsons. 2000. Can reduced salmonid population abundance be detected in time to limit management impacts? *Canadian Journal of Fisheries and Aquatic Sciences* 57:17-24.
- Hamilton, J.B., G.L. Curtis, S.M. Snedaker, and D.K. White. 2005. Distribution of anadromous fishes in the upper Klamath River watershed prior to hydropower dams – a synthesis of the historical evidence. *Fisheries* 30: 10-20.
- Hamlet, A.F. 2006. Hydrologic implications of 20th century warming and climate variability in the western U.S. Doctoral dissertation, University of Washington, Seattle, WA.
- Hankin, D.G. and G.H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. *Canadian Journal of Fisheries and Aquatic Sciences* 45:834-844.

- Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. *American Naturalist* 147: 527-541.
- Harig, A.L. and K.D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. *Ecological Applications* 12:535-551.
- Harig, A.L., K.D. Fausch, and M.K. Young. 2000. Factors influencing success of greenback cutthroat trout translocations. *North American Journal of Fisheries Management* 20:994-1004.
- Haroldson, M.A. and seven others. 2005. Changing numbers of spawning cutthroat trout in tributary streams of Yellowstone Lake and estimates of grizzly bears visiting streams from DNA. *Ursus* 16:167-180.
- Harris, J.L. 2004. Forest insect and disease conditions in the Rocky Mountain Region. USDA Forest Service Rocky Mountain Region, Renewable Resources, R2-04-03. Denver, CO.
- Harvey, B.C. 1998. Influence of large woody debris on retention, immigration, and growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream pools. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1902-1908.
- Harvey, B.C., R.J. Nakamoto, and J.L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult coastal cutthroat trout (*Oncorhynchus clarki clarki*) during fall and winter. *Canadian Journal of Fisheries and Aquatic Sciences* 56:2161-2166.
- Harvey, B.C., R.J. Nakamoto, and J.L. White. 2006. Reduced streamflow lowers dry-season growth of rainbow trout in a small stream. *Transactions of the American Fisheries Society* 135:998-1005.
- Hauer, F.R., G.C. Poole, J.T. Gangemi, and C.V. Baxter. 1999. Large woody debris in bull trout (*Salvelinus confluentus*) spawning streams of logged and wilderness watersheds in northwest Montana. *Canadian Journal of Fisheries and Aquatic Sciences* 56:915-924.
- Healey, M.C. and A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. *American Fisheries Society Symposium* 17:176-184.
- Heath, D.D., C. Busch, J. Kelly, and D.Y. Atagi. 2002. Temporal change in genetic structure and effective population size in steelhead trout (*Oncorhynchus mykiss*). *Molecular Ecology* 11:197-214.
- Heggberget, T.G. and T. Hesthagen. 1979. Population estimates of young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., by electrofishing in two small streams in north Norway. Report of the Institute of Freshwater Research Drottningholm 58:27-33.
- Heggenes, J., Å. Brabrand, and S.J. Saltveit. 1990. Comparison of three methods for studies of stream habitat use by young brown trout and Atlantic salmon. *Transactions of the American Fisheries Society* 119:101-111.
- Helfman, G.S. 1981. Twilight activities and temporal structure in a freshwater fish community. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1405-1420.
- Henderson, R.C., E.K. Archer, B.A. Bouwes, M.S. Coles-Ritchie, and J.L. Kershner. 2004. PACFISH/INFISH Biological Opinion: Effectiveness Monitoring Program seven-year status report 1998 through 2004. USDA Forest Service General Technical Report RMRS-GTR-162.
- Henderson, R.C., J.L. Kershner, and C.A. Toline. 2000. Timing and location of spawning of non-native wild rainbow trout and native cutthroat trout in the South Fork Snake River, Idaho, with implications for hybridization. *North American Journal of Fisheries Management* 20:584-596.
- Hendrickson, D.A. and 12 others. 2002. Mexican native trouts: a review of their history and current systematic and conservation status. *Reviews in Fish Biology and Fisheries* 12:273-316.
- Hendry, A.P. 2004. Selection against migrants contributes to the rapid evolution of ecologically-dependent reproductive isolation. *Evolutionary Ecology Research* 6:1219-1236.
- Hendry, A.P., V. Castaic, M.T. Kinnison, and T.P. Quinn. 2004. The evolution of philopatry and dispersal: homing versus straying in salmonids. Pages 52-91 in A.P. Hendry and S.C. Stearns, editors. *Evolution illuminated: salmon and their relatives*. Oxford University Press, Oxford.

- Hepworth, D.K., M.J. Ottenbacher, and C.B. Chamberlain. 2001. Occurrence of native Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in the Escalante River drainage, Utah. *Western North America Naturalist* 61: 129-138.
- Hepworth, D.K., M.J. Ottenbacher, and C.B. Chamberlain. 2002. A review of a quarter century of native trout conservation in southern Utah. *Intermountain Journal of Sciences* 8:125-142.
- Herger, L.G., W.A. Hubert, and M.K. Young. 1996. Comparison of habitat composition and cutthroat trout abundance at two flows in small mountain streams. *North American Journal of Fisheries Management* 16:294-301.
- Hessburg, P.F., E.E. Kuhlmann, and T.W. Swetnam. 2005. Examining the recent climate through the lens of ecology: inferences from temporal pattern analysis. *Ecological Applications* 15:440-457.
- Hesthagen, T. T. Forseth, O. Hegge, R. Saksgard, and J. Skurdal. 2004. Annual variability in the life-history characteristics of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in a subalpine Norwegian lake. *Hydrobiologia* 521:177-186.
- Hetzel, R. and A. Hampel. 2006. Long-term rates of faulting derived from cosmogenic nuclides and short-term variations caused by glacial-interglacial volume changes of glaciers and lakes. *International Journal of Modern Physics B* 20:261-276.
- Hickey, M.A. and G.P. Closs. 2006. Evaluating the potential of night spotlighting as a method for assessing species composition and brown trout abundance: a comparison with electrofishing in small streams. *Journal of Fish Biology* 69:1513-1523.
- Hickman, T. and R.F. Raleigh. 1982. Habitat suitability index models: cutthroat trout. U.S. Fish and Wildlife Service No. FWS/OBS-82/10.5.
- Higgins, J.V., M.T. Bryer, M.L. Khoury, and T.W. Fitzhugh. 2005. A freshwater classification approach for biodiversity conservation planning. *Conservation Biology* 19:432-445.
- Hilborn, R. and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, NJ.
- Hilderbrand, R.H. 2002. Simulating supplementation strategies for restoring and maintaining stream resident cutthroat trout populations. *North American Journal of Fisheries Management* 22:879-887.
- Hilderbrand, R.H. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. *Biological Conservation* 110:257-266.
- Hilderbrand, R.H. and J.L. Kershner. 2000. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho-Utah. *Transactions of the American Fisheries Society* 129:1160-1170.
- Hilderbrand, R.H. and J.L. Kershner. 2004. Influence of habitat type on food supply, selectivity, and diet overlap of Bonneville cutthroat trout and nonnative brook trout in Beaver Creek, Idaho. *North American Journal of Fisheries Management* 24:33-40.
- Hillman, T.W., J.W. Mullan, and J.S. Griffith. 1992. Accuracy of underwater counts of juvenile chinook salmon, coho salmon, and steelhead. *North American Journal of Fisheries Management* 12:598-603.
- Hirsch, C.L., S.E. Albeke, and T.P. Nesler. 2006. Range-wide status of Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*): 2005. Colorado Division of Wildlife, Denver, CO.
- Hitt, N.P., C.A. Frissell, C.C. Muhlfeld, and F.W. Allendorf. 2003. Spread of hybridization between native westslope cutthroat trout, *Oncorhynchus clarki lewisi*, and nonnative rainbow trout, *Oncorhynchus mykiss*. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1440-1451.
- Hixon, S.E., R.L. Leiby, J.P. Potyondy, B.B. Roper, W.R. Lorenz, and C.M. Knopp. 2004. *Aquatic ecological unit inventory technical guide*. USDA Forest Service, Washington Office, Ecosystem Management Coordination Staff. Washington, D.C.
- House, R. 1995. Temporal variation in abundance of an isolated population of cutthroat trout in western Oregon, 1981-1991. *North American Journal of Fisheries Management* 15:33-41.

- Howell, P.J. 2006. Effects of wildfire and subsequent hydrologic events on fish distribution and abundance in tributaries of North Fork John Day River. *North American Journal of Fisheries Management* 26:983-994.
- Hughes, N.F. 1992. Selection of positions by drift-feeding salmonids in dominance hierarchies: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1999-2008.
- Hunter, C.J. 1991. Better trout habitat: a guide to stream restoration and management. Island Press, Washington, D.C.
- Hyde, K. 2003. The use of wildfire burn severity mapping to indicate potential locations for gully rejuvenation, Bitterroot Valley, Montana. Master's thesis, University of Montana, Missoula, MT.
- Independent Scientific Advisory Board. 2003. A review of strategies for recovering tributary habitat. Northwest Power Planning Council, National Marine Fisheries Service, and Columbia River Basin Indian Tribes, 851 SW 6th Avenue, Suite 1100, Portland, OR.
- Inouye, D.W., B. Barr, K.B. Armitage, and B.D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences* 97:1630-1633.
- Intergovernmental Panel on Climate Change. 2007. Climate change 2007: the physical science basis. Summary for policymakers. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Available at: <http://www.ipcc.ch/SPM2feb07.pdf> (accessed 2 February 2007).
- Isaak, D.J. and W.A. Hubert. 2000. Are trout populations affected by reach-scale stream slope? *Canadian Journal of Fisheries and Aquatic Sciences* 57:468-477.
- Isaak, D.J. and W.A. Hubert. 2004. Nonlinear response of trout abundance to summer stream temperatures across a thermally diverse montane landscape. *Transactions of the American Fisheries Society* 133:1254-1259.
- Isaak, D.J. and R.F. Thurow. 2006. Network-scale spatial and temporal variation in Chinook salmon (*Oncorhynchus tshawytscha*) redd distributions: patterns inferred from spatially continuous replicate surveys. *Canadian Journal of Fisheries and Aquatic Sciences* 63:285-296.
- Isaak, D.J., R.F. Thurow, B.E. Rieman, and J.B. Dunham. 2003. Temporal variation in synchrony among chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 60:840-848.
- Jakober, M.J., T.E. McMahon, and R.F. Thurow. 2000. Diel habitat partitioning by bull charr and cutthroat trout during fall and winter in Rocky Mountain streams. *Environmental Biology of Fishes* 59:79-89.
- Jakober, M.J., T.E. McMahon, R.F. Thurow, and C.G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. *Transactions of the American Fisheries Society* 127:223-235.
- James, C. 2003. Conservation assessment for the Colorado River cutthroat trout in the Grand Mesa, Uncompahgre, and Gunnison National Forest, Colorado. Grand Mesa, Uncompahgre, and Gunnison National Forests, 2505 South Townsend Avenue, Montrose, CO. 15 p.
- James, F.C. 1999. Lessons learned from a study of habitat conservation planning. *BioScience*. 49:871-874.
- Jenkinson, R.G., K.A. Barnas, J.H. Braatne, E.S. Bernhardt, M.A. Palmer, J.D. Allan, and the National River Restoration Science Synthesis. 2006. Stream restoration databases and case studies: a guide to information resources and their utility in advancing the science and practice of restoration. *Restoration Ecology* 14: 177-186.
- Jensen, A.J. and B.O. Johnsen. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology* 13:778-785.
- Jensen, L.F., M.M. Hansen, J. Carlsson, V. Loeschcke, and K.-L. D. Mensberg. 2005. Spatial and temporal genetic differentiation and effective population size of brown trout (*Salmo trutta*, L.) in small Danish rivers. *Conservation Genetics* 6:615-621.

- Jespersen, D.M. 1981. A study of the effects of water diversion on the Colorado River cutthroat trout (*Salmo clarki pleuriticus*) in the drainage of the North Fork of the Little Snake River in Wyoming. Master's thesis, University of Wyoming, Laramie, WY.
- Johansen, M., J.M. Elliott, and A. Klemetsen. 2005. A comparative study of juvenile salmon density in 20 streams throughout a very large river system in northern Norway. *Ecology of Freshwater Fish* 14:96-110.
- Johnson, S.L. 2004. Factors influencing stream temperatures in small streams: substrate effects and a shading experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 61:913-923.
- Johnstone, H.C. and F.J. Rahel. 2003. Assessing temperature tolerance of cutthroat trout based on constant and cycling thermal regimes. *Transactions of the American Fisheries Society* 132:92-99.
- Jones, K.K., J.M. Dambacher, B.G. Lovatt, A.G. Talabere, and W. Bowers. 1998. Status of Lahontan cutthroat trout in the Coyote Lake basin, southeast Oregon. *North American Journal of Fisheries Management* 18:308-317.
- Jones, M.L. and J.D. Stockwell. 1995. A rapid assessment procedure for the enumeration of salmonine populations in streams. *North American Journal of Fisheries Management* 15:551-562.
- Jonsson, B. and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* 3:348-365.
- Jonsson, B., N. Jonsson, E. Brodtkorb, and P.-J. Ingebrigtsen. 2001. Life-history traits of brown trout vary with the size of small streams. *Functional Ecology* 15:310-317.
- Jonsson, E.R. and T. Antonsson. 2005. Emigration of age-1 Arctic charr, *Salvelinus alpinus*, into a brackish lagoon. *Environmental Biology of Fishes* 74:195-200.
- Jonsson, N., B. Jonsson, and L.P. Hansen. 1991. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology* 39:739-744.
- Jonzén, N., J.R. Rhodes, and H.P. Possingham. 2005. Trend detection in source-sink systems: when should sink habitats be monitored? *Ecological Applications* 15:326-334.
- Joyce, M.P. and W.A. Hubert. 2004. Spawning ecology of finespotted Snake River cutthroat trout in spring streams of the Salt River valley, Wyoming. *Western North American Naturalist* 64:78-85.
- Kaczynski, V.W. and F. Alvarado. 2006. Assessment of the southern range limit of North American coho salmon: difficulties in establishing natural range boundaries. *Fisheries* 31:374-391.
- Kanda, N., R.F. Leary, P. Spruell, and F.W. Allendorf. 2002. Molecular genetic markers identifying hybridization between Colorado River-greenback cutthroat trout complex and Yellowstone cutthroat trout or rainbow trout. *Transactions of the American Fisheries Society* 131:312-319.
- Karr, J.R. and six others. 2004. The effects of postfire salvage logging on aquatic ecosystems in the American West. *Bioscience* 54:1029-1033.
- Kaufmann, P.R., P. Levine, E.G. Robison, C. Seeliger, and D.V. Peck. 1999. Quantifying physical habitat in wadeable streams. U.S. Environmental Protection Agency, Washington, D.C. EPA/620/R-99/003.
- Kawaguchi, Y., Y. Taniguchi, and S. Nakano. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. *Ecology* 84:701-708.
- Keane, R.E., K.C. Ryan, T.T. Veblen, C. Allen, J. Logan, and B. Hawkes. 2002. The cascading effects of fire exclusion in Rocky Mountain ecosystems. Pages 133-152 in J. Baron, editor. *Rocky Mountain futures: an ecological perspective*. Island Press, Washington, D.C.
- Keeley, E.R. and J.W.A. Grant. 2001. Prey size of salmonid fishes in streams, lakes, and oceans. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1122-1132.
- Keleher, C.J. and F.J. Rahel. 1996. Thermal limits to salmonid distributions in the Rocky Mountain region and potential habitat loss due to global warming: a geographic information system (GIS) approach. *Transactions of the American Fisheries Society* 125:1-13.

- Keller, L.F. and D.M. Waller. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17: 230-241.
- Kennedy, B.M., D.P. Peterson, and K.D. Fausch. 2003. Different life histories of brook trout populations invading mid-elevation and high-elevation cutthroat trout streams in Colorado. *Western North American Naturalist* 63: 215-223.
- Kershner, J.L., C.M. Bischoff, and D.L. Horan. 1997. Population, habitat, and genetic characteristics of Colorado River cutthroat trout in wilderness and nonwilderness stream sections in the Uinta Mountains of Utah and Wyoming. *North American Journal of Fisheries Management* 17:1134-1143.
- Kershner, J.L., B.B. Roper, N. Bouwes, R. Henderson, and E. Archer. 2004. An analysis of stream habitat conditions in reference and managed watersheds on some federal lands within the Columbia River basin. *North American Journal of Fisheries Management* 24:1363-1375.
- Kinnison, M.T. and A.P. Hendry. 2004. Tempo and mode in salmon evolution. Pages 208-231 in A.P. Hendry and S.C. Stearns, editors. *Evolution illuminated: salmon and their relatives*. Oxford University Press, Oxford.
- Kittel, T.G.F., P.E. Thornton, J.A. Royle, and T.N. Chase. 2002. Climates of the Rocky Mountains: historical and future patterns. Pages 59-82 in J.S. Baron, editor. *Rocky Mountain futures: an ecological perspective*. Island Press, Washington, D.C.
- Klemetsen, A. and six others. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish* 12:1-59.
- Knapp, R.A. and K.R. Matthews. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. *Restoration Ecology* 6:207-213.
- Koizumi, I. and K. Maekawa. 2004. Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. *Freshwater Biology* 49:973-981.
- Kondolf, G.M. and M.G. Wolman. 1993. The sizes of salmonid spawning gravels. *Water Resources Research* 27: 2275-2285.
- Kondolf, G.M., G.F. Cada, M.J. Sale, and T. Felando. 1991. Distribution and stability of potential salmonid spawning gravels in steep boulder-bed streams of the eastern Sierra Nevada. *Transactions of the American Fisheries Society* 120:177-186.
- Korman, J. and P.S. Higgins. 1997. Utility of escapement time series data for monitoring the response of salmonid populations to habitat alteration. *Canadian Journal of Fisheries and Aquatic Sciences* 54:2058-2067.
- Koskinen, M.T., T.O. Haugen, and C.R. Primmer. 2002. Contemporary fisherian life-history evolution in small salmonid populations. *Nature* 419:826-830.
- Kritzer, J.P., C.R. Davies, and B.D. Mapstone. 2001. Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1557-1568.
- Krueger, C.C., A.J. Gharrett, T.R. Dehring, and F.W. Allendorf. 1981. Genetic aspects of fisheries rehabilitation programs. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1877-1881.
- Kruse, C.G., W.A. Hubert, and F.J. Rahel. 1997. Geomorphic influences on the distribution of Yellowstone cutthroat trout in the Absaroka Mountains, Wyoming. *Transactions of the American Fisheries Society* 126:418-427.
- Kruse, C.G., W.A. Hubert, and F.J. Rahel. 1998. Single-pass electrofishing predicts trout abundance in mountain streams with sparse habitat. *North American Journal of Fisheries Management* 18:940-946.
- Kulp, M.A. and S.E. Moore. 2000. Multiple electrofishing removals for eliminating rainbow trout in a small southern Appalachian stream. *North American Journal of Fisheries Management* 20:259-266.
- Labbe, T.R. and K.D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications* 10:1774-1791.

- Lackey, R.T., D.H. Lach, and S.L. Duncan. 2006. Policy options to reverse the decline of wild Pacific salmon. *Fisheries* 31:344-351.
- Lacy, R.C. 1997. Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* 78:320-335.
- Laikre, L. and seven others. 2002. Spatial and temporal population structure of sea trout at the Island of Gotland, Sweden, delineated from mitochondrial DNA. *Journal of Fish Biology* 60:49-71.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.
- Langlois, D., J. Cameron, C. S. Hutchinson, M. Japhet, D. Smith, and J. Castellano. 1994. Colorado River cutthroat trout conservation strategy for southwestern Colorado. Colorado Division of Wildlife, Montrose, Colorado. 42 p.
- Larsen, D.P., P.R. Kaufmann, T.M. Kincaid, and N.S. Urquhart. 2004. Detecting persistent change in the habitat of salmon-bearing streams in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 283-291.
- Larson, G.L., S.E. Moore, and B. Carter. 1995. Ebb and flow of encroachment by nonnative rainbow trout in a small stream in the southern Appalachian Mountains. *Transactions of the American Fisheries Society* 124:613-622.
- Latterell, J.J., K.D. Fausch, C. Gowan, and S.C. Riley. 1998. Relationship of trout recruitment to snowmelt runoff flows and adult trout abundance in six Colorado mountain streams. *Rivers* 6:240-250.
- Leary, R.F., F.W. Allendorf, and G.K. Sage. 1995. Hybridization and introgression between introduced and native fish. *American Fisheries Society Symposium* 15:91-101.
- Leary, R.F., F.W. Allendorf, S.R. Phelps, and K.L. Knudsen. 1987. Genetic divergence and identification of seven cutthroat trout subspecies and rainbow trout. *Transactions of the American Fisheries Society* 116:580-587.
- Leary, R.F., W.R. Gould, and G.K. Sage. 1996. Success of basibranchial teeth in indicating pure populations of rainbow trout and failure to indicate pure populations of westslope cutthroat trout. *North American Journal of Fisheries Management* 16:210-213.
- Lee, D., J. Sedell, B. Rieman, R. Thurow, and J. Williams. 1997. Assessment of the condition of aquatic ecosystems in the interior Columbia River Basin. Chapter 4. Pages 1058-1496 *in* T.M. Quigley and S.J. Arbelbide, editors. An assessment of ecosystem components in the interior Columbia Basin. Volume III. USDA Forest Service General Technical Report PNW-GTR-405.
- Legg, C.J. and L. Nagy. 2006. Why most conservation monitoring is, but need not be, a waste of time. *Journal of Environmental Management* 78:194-199.
- Leopold, A. 1949. *A sand county almanac and sketches here and there*. Oxford University Press, New York.
- Leslie, H., M. Ruckelshaus, I.R. Ball, S. Andelman, and H.P. Possingham. 2003. Using siting algorithms in the design of marine reserve networks. *Ecological Applications* 13(Supplement):S185-S198.
- Levin, P.S., R.W. Zabel, and J.G. Williams. 2001. The road to extinction is paved with good intentions: negative associations of fish hatcheries with threatened salmon. *Proceedings of the Royal Society of London B* 268:1-6.
- Levin, P.S., S. Achord, B.E. Feist, and R.W. Zabel. 2002. Non-indigenous brook trout and the demise of Pacific salmon: a forgotten threat? *Proceedings of the Royal Society of London Series B Biological Sciences* 269: 1663-1670.
- Lewynsky, V.A. 1986. Evaluation of special angling regulations in the Coeur d'Alene River trout fishery. Master's thesis, University of Idaho, Moscow, ID.
- Libosvářský, J. 1990. Notes on electric fishing mainly on the probability of capture. Pages 140-144 *in* I.G., Cowx, editor. *Developments in electric fishing*. Fishing News Books, Oxford.
- Licciardi, J.M., P.U. Clark, E.J. Brook, D. Elmore, and P. Sharma. 2004. Variable responses of western U.S. glaciers during the last deglaciation. *Geology* 32:81-84.

- Lichatowich, J., L. Mobrand, and L. Lestelle. 1999. Depletion and extinction of Pacific salmon (*Oncorhynchus* spp.): a different perspective. *ICES Journal of Marine Science* 56:467-472.
- Lindemann, J.D. and W.L. Baker. 2001. Attributes of blowdown patches from a severe wind event in the Southern Rocky Mountains, USA. *Landscape Ecology* 16:313-325.
- Lindenmeyer, D.B., H.P. Possingham, R.C. Lacy, M.A. McCarthy, and M.L. Pope. 2003. How accurate are population models? Lessons from landscape-scale tests in a fragmented system. *Ecology Letters* 6:41-47.
- Lindstrom, J.W. 2003. Habitat selection and movements of adult cutthroat trout and brook trout from fall through winter in a meandering alluvial-valley stream. Master's thesis, University of Wyoming, Laramie.
- Lobón-Cerviá, J. 2004. Discharge-dependent covariation patterns in the population dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage. *Canadian Journal of Fisheries and Aquatic Sciences* 61:1929-1939.
- Lobón-Cerviá, J. 2005. The importance of recruitment for the production dynamics of stream-dwelling brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* 62:2484-2493.
- Lobón-Cerviá, J. and E. Mortensen. 2005. Population size in stream-living juveniles of lake-migratory brown trout *Salmo trutta* L.: the importance of stream discharge and temperature. *Ecology of Freshwater Fish* 14:394-401.
- Lobón-Cerviá, J. and C.G. Utrilla. 1993. A simple model to determine stream trout (*Salmo trutta* L.) densities based on one removal with electrofishing. *Fisheries Research* 15:369-378.
- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80:298-310.
- Ludwig, D. and C. J. Walters. 2002. Fitting population viability analysis into adaptive management. Pages 511-520 in S.R. Beissinger and D.R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, IL.
- Lundquist, C.J., J.M. Diehl, E. Harvey, and L.W. Botsford. 2002. Factors affecting implementation of recovery plans. *Ecological Applications* 12:713-718.
- Lyon, L.J. 1984. The Sleeping Child burn—21 years of postfire change. USDA Forest Service Research Paper INT-330.
- Madole, R.F. 1976. Glacial geology of the Front Range, Colorado. Pages 297-318 in W.C. Mahaney, editor. *Quaternary stratigraphy of North America*. Dowden, Hutchinson, and Ross, Stroudsburg, PA.
- Madole, R.F., D.P. Van Sistine, and J.A. Michael. 1998. Pleistocene glaciation in the Upper Platte River drainage basin, Colorado. U.S. Geological Survey Geologic Investigations Series I-2644.
- Magee, J.P., T.E. McMahon, and R.F. Thurow. 1996. Spatial variation in spawning habitat of cutthroat trout in a sediment-rich stream basin. *Transactions of the American Fisheries Society* 125:768-779.
- Mahon, R. 1980. Accuracy of catch-effort methods for estimating fish density and biomass in streams. *Environmental Biology of Fishes* 5:343-363.
- Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78:1069-1079.
- Margules, C.R. and R.L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.
- Martin, M.A., D.K. Shiozawa, E.J. Loudenslager, and J.N. Jensen. 1985. Electrophoretic study of cutthroat trout populations in Utah. *Great Basin Naturalist* 45:677-687.
- Martinez, A.M. 1988. Identification and status of Colorado River cutthroat trout in Colorado. *American Fisheries Society Symposium* 4:81-89.
- Mason, J.C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *Journal of Wildlife Management* 40:775-788.
- Maxell, B.A. 1999. A power analysis on the monitoring of bull trout stocks using redd counts. *North American Journal of Fisheries Management* 19:860-866.

- Maxwell, D. and S. Jennings. 2005. Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. *Journal of Applied Ecology* 42:25-37.
- May, C.L. and R.E. Gresswell. 2003. Large wood recruitment and redistribution in headwater streams in the southern Oregon Coast Range, U.S.A. *Canadian Journal of Forest Research* 33:1352-1362.
- McAlpine, C.A., T.A. Spies, P. Norman, and A. Peterson. 2007. Conserving forest biodiversity across multiple land ownerships: lessons from the Northwest Forest Plan and the Southeast Queensland regional forests agreement (Australia). *Biological Conservation* 134:580-592.
- McElhany, P., M.H. Ruckelshaus, M.J. Ford, T.C. Wainwright, and E.P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. NOAA Technical Memorandum NMFS-NWFSC-42.
- McGrath, C.C. 2004. Trophic roles of native greenback cutthroat trout and non-native brook trout in montane streams of Colorado. Doctoral dissertation, University of Colorado, Boulder.
- McGrath, C.C. and W.M. Lewis, Jr. In press. Competition and predation as mechanisms for displacement of greenback cutthroat trout by brook trout. *Transactions of the American Fisheries Society*.
- McHugh, P. and P. Budy. 2005. An experimental evaluation of competitive and thermal effects on brown trout (*Salmo trutta*) and Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) performance along an altitudinal gradient. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2784-2795.
- McHugh, P. and P. Budy. 2006. Experimental effects on nonnative brown trout on the individual- and population-level performance of native Bonneville cutthroat trout. *Transactions of the American Fisheries Society* 135: 1441-1455.
- McIntosh, B.A., J.R. Sedell, R.F. Thurow, S.E. Clarke, and G.L. Chandler. 2000. Historical changes in pool habitats in the Columbia River basin. *Ecological Applications* 10:1478-1496.
- McIntyre, J.D. and B.E. Rieman. 1995. Westslope cutthroat trout. Pages 1-15 in M. K. Young, technical editor. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-GTR-256.
- McKay, J.K., C.E. Christian, S. Harrison, and K.J. Rice. 2005. "How local is local?" – A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology* 13:432-440.
- Mears, B., Jr. 1987. Late Pleistocene periglacial wedge sites in Wyoming: an illustrated compendium. Geological Survey of Wyoming, Laramie, Wyoming. Memoir 3.
- Mears, B., Jr. 2001. Glacial records in the Medicine Bow Mountains and Sierra Madre of southern Wyoming and adjacent Colorado, with a traveler's guide to their sites. Wyoming State Geological Survey, Laramie, Wyoming. Public Information Circular 41.
- Meehan, W.R., editor. 1991. Influences of forest and rangeland management on salmonid fishes and their habitat. American Fisheries Society, Bethesda, Maryland. Special Publication 19.
- Meeuwig, M.H., J.B. Dunham, J.P. Hayes, and G.L. Vinyard. 2004. Effects of constant and cyclical thermal regimes on growth and feeding of juvenile cutthroat trout of variable sizes. *Ecology of Freshwater Fish* 13:208-216.
- Meir, E., S. Andelman, and H.P. Possingham. 2004. Does conservation planning matter in a dynamic and uncertain world? *Ecology Letters* 7:615-622.
- Menounos, B. and M.A. Reasoner. 1997. Evidence for cirque glaciation in the Colorado Front Range during the Younger Dryas Chronozone. *Quaternary Research* 48:38-47.
- Mesa, M.G. and C.B. Schreck. 1989. Electrofishing mark-recapture and depletion methodologies evoke behavioral and physiological changes in cutthroat trout. *Transactions of the American Fisheries Society* 118:644-658.
- Metcalf, J. and A. Martin. 2007. Post-doctoral researcher and Associate Professor, Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO. Personal communication.

- Metcalf, J.L., and eight others. In press. Across the great divide: Genetic forensics reveals misidentification of endangered cutthroat trout populations. *Molecular Ecology*.
- Meyer, K.A., J.A. Lamansky, Jr., and D.J. Schill. 2006a. Evaluation of an unsuccessful brook trout electrofishing removal project in a small Rocky Mountain stream. *North American Journal of Fisheries Management* 26: 849-860.
- Meyer, K.A., D.J. Schill, F.S. Elle, and J.A. Lamansky, Jr. 2003. Reproductive demographics and factors that influence length at sexual maturity of Yellowstone cutthroat trout in Idaho. *Transactions of the American Fisheries Society* 132:183-195.
- Meyer, K. 2006. Principal Fisheries Research Manager, Idaho Department of Fish and Game, Boise, ID. Personal communication.
- Meyer, K.A., D.J. Schill, J.A. Lamansky, Jr., M.R. Campbell, and C.C. Kozfkay. 2006b. Status of Yellowstone cutthroat trout in Idaho. *Transactions of the American Fisheries Society* 135:1329-1347.
- Miller, D. 2007. Fisheries Management Coordinator, Wyoming Game and Fish Department, Cheyenne, WY. Personal communication.
- Miller, D., C. Luce, and L. Benda. 2003. Time, space, and episodicity of physical disturbance in streams. *Forest Ecology and Management* 178:121-140.
- Miller, R.B. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. *Journal of the Fisheries Research Board of Canada* 14:687-691.
- Mills, L.S., D.F. Doak, and M.J. Wisdom. 1999. The reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* 13:815-829.
- Mills, L.S. and M.S. Lindbergh. 2002. Sensitivity analysis to evaluate the consequences of conservation actions. Pages 338-366 in S.R. Beissinger and D.R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, IL.
- Minckley, W.L. 1999. Ecological review and management recommendations for recovery of the endangered Gila topminnow. *Great Basin Naturalist* 59:230-244.
- Minckley, W.L., D.A. Hendrickson, and C.E. Bond. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. Pages 519-614 in C.H. Hocutt and E.O. Wiley, editors. *The zoogeography of North American freshwater fishes*. John Wiley & Sons, NY.
- Minns, C.K., J.R.M. Kelso, and R.G. Randall. 1996. Detecting the response of fish to habitat alterations in freshwater ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1):403-414.
- Minshall, G.W. and J.T. Brock. 1991. Observed and anticipated effects of forest fire on Yellowstone stream ecosystems. Pages 123-135 in R.B. Keiter and M.S. Boyce, editors. *The Greater Yellowstone Ecosystem: redefining America's wilderness heritage*. Yale University Press, New Haven, CT.
- Miranda, L.E. and C.R. Dolan. 2003. Test of a power transfer model for standardized electrofishing. *Transactions of the American Fisheries Society* 132:1179-1185.
- Miranda, L.E. and C.R. Dolan. 2004. Electrofishing power requirements in relation to duty cycle. *North American Journal of Fisheries Management* 24:55-62.
- Mitro, M.G. and A.V. Zale. 2000. Predicting fish abundance using single-pass removal sampling. *Canadian Journal of Fisheries and Aquatic Sciences* 57:951-961.
- Mobrand, L.E. and nine others. 2005. Hatchery reform in Washington state: principles and emerging issues. *Fisheries* 30(6):11-23.
- Mohler, J.W., M.J. Millard, and J.W. Fletcher. 2002. Predation by captive wild brook trout on calcein-marked versus nonmarked Atlantic salmon fry. *North American Journal of Fisheries Management* 22:223-228.

- Molles, M.C. 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. *Ecology* 63:1-6.
- Monroe, J.S., B.J.C. Laabs, J.D. Shakun, B.S. Singer, D.M. Mickelson, K.A. Refsnider, and M.W. Caffee. 2006. Latest Pleistocene advance of alpine glaciers in the southwestern Uinta Mountains, Utah, USA: Evidence for the influence of local moisture sources. *Geology* 34:841-844.
- Montgomery, D.R. and L.H. MacDonald. 2002. Diagnostic approach to stream channel assessment and monitoring. *Journal of the American Water Resources Association* 38:1-16.
- Montgomery, D.R., B.D. Collins, J.M. Buffington, and T.B. Abbe. 2003. Geomorphic effects of wood in rivers. *American Fisheries Society Symposium* 37:21-47.
- Moore, K.M.S. and S.V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1921-1930.
- Morinville, G.R. and J.B. Rasmussen. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 60:401-410.
- Morita, K. and S. Yamamoto. 2002. Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology* 16:1318-1323.
- Morita, K. and A. Yokota. 2002. Population viability of stream-resident salmonids after habitat fragmentation: a case study with white-spotted charr (*Salvelinus leucomaenis*) by an individual based model. *Ecological Modelling* 155:85-94.
- Morris, W.F. and D.F. Doak. 2004. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, MA.
- Mote, P.W., A.F. Hamlet, M.P. Clark, and D.P. Lettenmaier. 2005. Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society* 86:39-49.
- Mullner, S.A., W.A. Hubert, and T.A. Wesche. 1998. Snorkeling as an alternative to depletion electrofishing for estimating abundance and length-class frequencies of trout in small streams. *North American Journal of Fisheries Management* 18:947-953.
- Munro, A.R., T.E. McMahon, and J.R. Ruzyski. 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. *Canadian Journal of Fisheries and Aquatic Sciences* 62:79-87.
- Myers, R.A., G. Mertz, and J. Bridson. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1400-1407.
- Naiman, R.J., J.M. Melillo, and J.E. Hobbie. 1986. Ecosystem alternation of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254-1269.
- Nakano, S., S. Kitano, K. Nakai, and K.D. Fausch. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. *Environmental Biology of Fishes* 52:345-355.
- NatureServe. 2006. Available at: <http://www.natureserve.org/explorer/>. Accessed 27 October 2006.
- Neely, B. and 12 others. 2001. Southern Rocky Mountains: an ecoregional assessment and conservation blueprint. Prepared by The Nature Conservancy with support from the U.S. Forest Service, Rocky Mountain Region, Colorado Division of Wildlife, and Bureau of Land Management.
- Nehring, R.B. and R.M. Anderson. 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the physical habitat simulation system. *Rivers* 4:1-19.
- Nehring, R.B. and P.G. Walker. 1996. Whirling disease in the wild: the new reality in the intermountain West. *Fisheries* 21(6):28-30.

- Nelson, M.L., T.E. McMahon, and R.F. Thurow. 2002. Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. *Environmental Biology of Fishes* 64:321-332.
- Neville, H.M., J.B. Dunham, and M.M. Peacock. 2006a. Landscape attributes and life history variability shape genetic structure of trout populations in a stream network. *Landscape Ecology* 21:901-916.
- Neville, H.M., J.B. Dunham, and M. Peacock. 2006b. Assessing connectivity in salmonid fishes with DNA microsatellite markers. Pages 318-342 in K.R. Crooks and M. Sanjayan, editors. *Connectivity conservation*. Cambridge University Press, London.
- Nickum, M., P. Mazik, J. Nickum, and D. MacKinlay, editors. 2004. *Propagated fish in resource management*. American Fisheries Society Symposium 44, Bethesda, Maryland.
- Nielsen, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Transactions of the American Fisheries Society* 121:617-634.
- Nielsen, J.L. 1998. Scientific sampling effects: electrofishing California's endangered fish populations. *Fisheries* 23(12):6-12.
- Nielsen, J.L. and G.K. Sage. 2001. Microsatellite analyses of the trout of northwest Mexico. *Genetica* 111:269-278.
- Nielsen, J.L. and G.K. Sage. 2002. Population genetic structure in Lahontan cutthroat trout. *Transactions of the American Fisheries Society* 131:376-388.
- Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology* 41:413-426.
- Northcote, T.G. 1992. Migration and residency in stream salmonids: some ecological considerations and evolutionary consequences. *Nordic Journal of Freshwater Resources* 67:5-17.
- Northcote, T.G. 1997. Potamodromy in Salmonidae--living and moving in the fast lane. *North American Journal of Fisheries Management* 17:1029-1045.
- Novinger, D.C. 2000. Reversals in competitive ability: do cutthroat trout have a thermal refuge from competition with brook trout? Doctoral dissertation, University of Wyoming, Laramie, WY.
- Oakley, T.H. and R.B. Phillips. 1999. Phylogeny of salmonine fishes based on growth hormone introns: Atlantic (*Salmo*) and Pacific (*Oncorhynchus*) salmon are not sister taxa. *Molecular Phylogeny and Evolution* 11: 381-393.
- Oberholtzer, M. 1987. A fisheries survey of the Little Snake River drainage, Carbon County, Wyoming. Administrative Report. Project 5086-01-8501. Wyoming Game and Fish Department, Cheyenne, WY.
- Oberholtzer, M. 1990. Current status of Colorado River cutthroat trout in the Little Snake River enclave. Administrative Report. Project 5090-28-8501. Wyoming Game and Fish Department, Cheyenne, WY.
- Olden, J.D. and D.A. Jackson. 2002. A comparison of statistical approaches for modelling fish species distributions. *Freshwater Biology* 47:1976-1995.
- O'Grady, J.J., B.W. Brook, D.H. Reed, J.D. Ballou, D.W. Tonkyn, and R. Frankham. 2006. Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biological Conservation* 133:42-51.
- Ostberg, C.O. and R.J. Rodriguez. 2006. Hybridization and cytonuclear associations among native westslope cutthroat trout, introduced rainbow trout, and their hybrids within the Stehekin River drainage, North Cascades National Park. *Transactions of the American Fisheries Society* 924-942.
- Østergaard, S., M.M. Hansen, V. Loeschcke, and E.E. Nielsen. 2003. Long-term temporal changes of genetic composition in brown trout (*Salmo trutta* L.) populations inhabiting an unstable environment. *Molecular Ecology* 12:3123-3135.
- Overton, C.K., S.P. Wollrab, B.C. Roberts, and M.A. Radko. 1997. R1/R4 (Northern/Intermountain Regions) fish and fish habitat standard inventory procedures handbook. USDA Forest Service General Technical Report INT-346.

- Palm, S., L. Laikre, P.E. Jorde, and N. Ryman. 2003. Effective population size and temporal genetic change in stream resident brown trout (*Salmo trutta*, L.). *Conservation Genetics* 4:249-264.
- Palmer, M.A. and 21 others. 2005. Standards for ecologically successful river restoration. *Journal of Applied Ecology* 42:208-217.
- Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.
- Paroz, Y.M. 2005. Population attributes and landscape scale habitat associations of Rio Grande cutthroat trout (*Oncorhynchus clarki virginalis*). Master's thesis, New Mexico State University, Las Cruces, NM.
- Parrett, C., S.H. Cannon, and K.L. Pierce. 2003. Wildfire-related floods and debris flows in Montana in 2000 and 2001. U.S. Geological Survey Water-Resources Investigation Report 03-4319.
- Paul, A.J. and J.R. Post. 2001. Spatial distribution of native and nonnative salmonids in streams of the eastern slopes of the Canadian Rocky Mountains. *Transactions of the American Fisheries Society* 130:417-430.
- Paul, A.J., J.R. Post, and J.D. Stelfox. 2003. Can anglers influence the abundance of native and nonnative salmonids in a stream from the Canadian Rocky Mountains? *North American Journal of Fisheries Management* 23:109-119.
- Peacock, M.M. and V. Kirchoff. 2004. Assessing the conservation value of hybridized cutthroat trout populations in the Quinn River drainage, Nevada. *Transactions of the American Fisheries Society* 133:309-325.
- Peck, D.V., J.M. Lazorchak, and D.J. Klemm, editors. 2001. Environmental monitoring and assessment program—surface waters: Western pilot study field operations manual for wadeable streams. U.S. Environmental Protection Agency, Washington, D.C. Available at: <http://www.epa.gov/emap/html/pubs/docs/groupdocs/surfwatr/field/ewwsm01.html>.
- Pepin, D.M., N.L. Poff, and J.S. Baron. 2002. Ecological effects of resource development in running waters. Pages 113-132 in J.S. Baron, editor. *Rocky Mountain futures: an ecological perspective*. Island Press, Washington, D.C.
- Perry, R.W., M.J. Bradford, and J.A. Grout. 2003. Effects of disturbance on contribution of energy sources to growth of juvenile chinook salmon (*Oncorhynchus tshawytscha*) in boreal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 60:390-400.
- Pess, G.R., D.R. Montgomery, E.A. Steel, R.E. Bilby, B.E. Feist, and H.M. Greenberg. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash., U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* 59:613-623.
- Peterman, R.M. 1990. Statistical power analysis can improve fisheries research and management. *Canadian Journal of Fisheries and Aquatic Sciences* 47:2-15.
- Peterman, R.M. and M.J. Bradford. 1987. Statistical power of trends in fish abundance. *Canadian Journal of Fisheries and Aquatic Sciences* 44:1879-1889.
- Peterson, D.P. 2002. Population ecology of an invasion: demography, dispersal, and effects of nonnative brook trout on native cutthroat trout. Doctoral dissertation, Colorado State University, Fort Collins.
- Peterson, D.P. and K.D. Fausch. 2003. Upstream movement by brook trout (*Salvelinus fontinalis*) promotes invasion of native cutthroat trout (*Oncorhynchus clarki*) habitat. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1502-1516.
- Peterson, D.P., K.D. Fausch, and G.C. White. 2004a. Population ecology of an invasion: effects of brook trout on native cutthroat trout. *Ecological Applications* 14:754-772.
- Peterson, J.T., N.P. Banish, and R.F. Thurow. 2005. Are block nets necessary?: movement of stream-dwelling salmonids in response to three common survey methods. *North American Journal of Fisheries Management* 25:732-743.

- Peterson, J.T. and J. Dunham. 2003. Combining inferences from models of capture efficiency, detectability, and suitable habitat to classify landscapes for conservation of threatened bull trout. *Conservation Biology* 17: 1070-1077.
- Peterson, J., J. Dunham, P. Howell, S. Bonar, and R. Thurow. 2002. Interim protocol for determining bull trout presence. Western Division of the American Fisheries Society.
- Peterson, J.T., R.F. Thurow, and J.W. Guzevich. 2004b. An evaluation of multipass electrofishing for estimating the abundance of stream-dwelling salmonids. *Transactions of the American Fisheries Society* 133:462-475.
- Peterson, N.P. and C.J. Cederholm. 1984. A comparison of the removal and mark-recapture methods of population estimation for juvenile coho salmon in a small stream. *North American Journal of Fisheries Management* 4: 99-102.
- Pettersson, J.C.E., M.M. Hansen, and T. Bohlin. 2001. Does dispersal from landlocked trout explain the coexistence of resident and migratory trout females in a small stream? *Journal of Fish Biology* 58:487-495.
- Petty, J.T., P.J. Lamothe, and P.M. Mazik. 2005. Spatial and seasonal dynamics of brook trout populations inhabiting a central Appalachian watershed. *Transactions of the American Fisheries Society* 134:572-587.
- Pierce, K.L. 2004. Pleistocene glaciations of the Rocky Mountains. Pages 63-76 in A. R. Gillespie, S. C. Porter, and B. F. Atwater, editors. *The Quaternary Period in the United States*. Elsevier, Amsterdam.
- Platt, J.R. 1964. Strong inference. *Science* 146:347-353.
- Platts, W.S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. *Fisheries* 4:5-9.
- Platts, W.S. and R.L. Nelson. 1988. Fluctuations in trout populations and their implications for land-use evaluations. *North American Journal of Fisheries Management* 8:333-345.
- Poole, G.C., C.A. Frissell, and S.C. Ralph. 1997. In-stream habitat unit classification: inadequacies for monitoring and some consequences for management. *Journal of the American Water Resources Association* 33:879-896.
- Pressey, R.L. 1994. *Ad hoc* reservations: forward or backward steps in developing representative reserve systems? *Conservation Biology* 8:662-668.
- Pritchard, V.L., K. Jones, and D.E. Cowley. 2007a. Estimation of introgression in cutthroat trout populations using microsatellites. *Conservation Genetics* (available online 13 February 2007).
- Pritchard, V.L., K. Jones, and D.E. Cowley. 2007b. Genetic diversity within fragmented cutthroat trout populations. *Transactions of the American Fisheries Society* 136:606-623.
- Propst, D.L. and J.A. Stefferud. 1997. Population dynamics of Gila trout in the Gila River drainage of the southwestern United States. *Journal of Fish Biology* 51:1137-1154.
- Propst, D.L., J.A. Stefferud, and P.R. Turner. 1992. Conservation and status of Gila trout, *Oncorhynchus gilae*. *The Southwestern Naturalist* 37:117-125.
- Putnam, M. 1992. A review of the nature, function, variability, and supply of pigments in salmonid fish. European Aquaculture Society, Special Publication.
- Quinlan, R.E. 1980. A study of the biology of the Colorado River cutthroat trout (*Salmo clarki pleuriticus*) population in the North Fork of the Little Snake River drainage in Wyoming. Master's thesis, University of Wyoming, Laramie, WY.
- Quinn, T.P. 2005a. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Washington.
- Quinn, T.P. 2005b. Comment: Sperm competition in salmon hatcheries—the need to institutionalize genetically benign spawning protocols. *Transactions of the American Fisheries Society* 134:1490-1494.
- Quist, M. and W.A. Hubert. 2004. Bioinvasive species and the preservation of cutthroat trout in the western United States: ecological, social, and economic issues. *Environmental Science and Policy* 7:303-313.

- Quist, M., K.G. Gerow, M.R. Bower, and W.A. Hubert. 2006. Random versus fixed-site sampling when monitoring relative abundance of fishes in headwater streams of the upper Colorado River basin. *North American Journal of Fisheries Management* 26:1011-1019.
- Rahel, F.J. 2004. Unauthorized fish introductions: fisheries management of the people, for the people, or by the people? *American Fisheries Society Symposium* 44:431-444.
- Rahel, F.J. and N.P. Nibbelink. 1999. Spatial patterns in relations among brown trout (*Salmo trutta*) distribution, summer air temperature, and stream size in Rocky Mountain streams. *Canadian Journal of Fisheries and Aquatic Sciences* 56(supplement 1):43-51.
- Railsback, S.F., B.C. Harvey, R.H. Lamberson, D.E. Lee, N.J. Claasen, and S. Yoshihara. 2002. Population-level analysis and validation of an individual-based cutthroat trout model. *Natural Resource Modeling* 15:83-110.
- Randall, R.G. 1990. Effect of water temperature, depth, conductivity and survey area on the catchability of juvenile Atlantic salmon by electric fishing in New Brunswick streams. Pages 79-90 in I.G., Cowx, editor. *Developments in electric fishing*. Fishing News Books, Oxford.
- Reeve, T., J. Lichatowich, W. Towey, and A. Duncan. 2006. Building science and accountability into community-based restoration: can a new funding approach facilitate effective and accountable restoration? *Fisheries* 31:17-24.
- Reeves, G.H. and nine others. 2003a. Aquatic and riparian effectiveness monitoring plan for the Northwest Forest Plan. USDA Forest Service General Technical Report PNW-GTR-577.
- Reeves, G.H., K.M. Burnett, and E.V. McGarry. 2003b. Sources of large wood in the main stem of a fourth-order watershed in coastal Oregon. *Canadian Journal of Forest Research* 33:1363-1370.
- Reeves, G.H., L.E. Benda, K.M. Burnett, P.A. Bisson, and J.R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium* 17:334-349.
- Reeves, G.H., D.B. Hohler, B.E. Hansen, F.H. Everest, J.R. Sedell, T.L. Hickman, and D. Shively. 1997. Fish habitat restoration in the Pacific Northwest: Fish Creek of Oregon. Pages 335-359 in J.E. Williams, C.A. Wood, and M.P. Dombeck, editors. *Watershed restoration: principles and practices*. American Fisheries Society, Bethesda, MD.
- Remmick, R. 1982. A survey of native cutthroat populations and associated stream habitats in the Bridger-Teton National Forest. Wyoming Game and Fish Department, Cheyenne.
- Reynolds, J.B. 1996. Electrofishing. Pages 221-253 in B.R. Murphy and D.W. Willis, editors. *Fisheries techniques*. 2nd edition. American Fisheries Society, Bethesda, MD.
- Rich, Jr. C.F., T.E. McMahon, B.E. Rieman, and W.L. Thompson. 2003. Local-habitat, watershed, and biotic features associated with bull trout occurrence in Montana streams. *Transactions of the American Fisheries Society* 132: 1053-1064.
- Richmond, A.D. and K.D. Fausch. 1995. Characteristics and function of large woody debris in subalpine Rocky Mountain streams in the northern Colorado. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 1789-1802.
- Richter, B.D., R. Mathews, D.L. Harrison, and R. Wigington. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications* 13:206-224.
- Rieman, B., D. Lee, D. Burns, R. Gresswell, M. Young, R. Stowell, J. Rinne, and P. Howell. 2003. Status of native fishes in the western United States and issues for fire and fuels management. *Forest Ecology and Management* 178:197-211.
- Rieman, B.E. and F.W. Allendorf. 2001. Effective population size and genetic conservation criteria for bull trout. *North American Journal of Fisheries Management* 21:756-764.
- Rieman, B.E. and J. Clayton. 1997. Wildfire and native fish: issues of forest health and conservation of sensitive species. *Fisheries* 22(11):6-15.

- Rieman, B.E. and J.B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. *Ecology of Freshwater Fish* 9:51-64.
- Rieman, B.E. and J.D. McIntyre. 1996. Spatial and temporal variability in bull trout redd counts. *North American Journal of Fisheries Management* 16:132-141.
- Rieman, B.E., D.L. Myers, and R.L. Nielsen. 1994. Use of otolith microchemistry to discriminate *Oncorhynchus nerka* of resident and anadromous origin. *Canadian Journal of Fisheries and Aquatic Sciences* 51:68-77.
- Riley, S.C. and K.D. Fausch. 1992. Underestimation of trout population size by maximum-likelihood removal estimates in small streams. *North American Journal of Fisheries Management* 12:768-776.
- Riley, S.C., R.L. Haedrich, and R.J. Gibson. 1993. Negative bias in removal estimates of Atlantic salmon parr relative to stream size. *Journal of Freshwater Ecology* 8:97-101.
- Rinne, J.N. 1996. Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States. *North American Journal of Fisheries Management* 16:653-658.
- Rinne, J.N. 1999. Fish and grazing relationships: the facts and some pleas. *Fisheries* 24(8):12-21.
- Rinne, J.N., W.L. Minckley, and J.N. Hanson. 1981. Chemical treatment of Ord Creek, Apache County, Arizona, to re-establish Arizona trout. *Journal of the Arizona-New Mexico Academy of Science* 16:74-78.
- Roberts, C.M. and 11 others. 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecological Applications* 13(Supplement):S215-S228.
- Robson, D.S. and H.A. Regier. 1964. Sample size in Petersen mark-recapture experiments. *Transactions of the American Fisheries Society* 93:215-226.
- Rodgers, J.D., M.F. Solazzi, S.L. Johnson, and M.A. Buckman. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. *North American Journal of Fisheries Management* 12: 79-86.
- Roghair, C.N., C.A. Dolloff, and M.K. Underwood. 2002. Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the American Fisheries Society* 131:718-730.
- Romero, N., R.E. Gresswell, and J. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarki*) diet and prey in a gradient of deciduous canopies. *Canadian Journal of Fisheries and Aquatic Sciences* 62:1797-1807.
- Roni, P., editor. 2005. Monitoring stream and watershed restoration. American Fisheries Society, Bethesda, MD.
- Roni, P. and A. Fayram. 2000. Estimating winter salmonid abundance in small western Washington streams: a comparison of three techniques. *North American Journal of Fisheries Management* 20:683-692.
- Roni, P., T.J. Beechie, R.E. Bilby, F.E. Leonetti, M.M. Pollock, and G.R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. *North American Journal of Fisheries Management* 22:1-20.
- Root, T.L., J.T. Price, K.R. Hall, S.H. Schneider, C. Rosenzweig, and J.A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57-60.
- Roper, B.B. and D.L. Scarnecchia. 1995. Observer variability in classifying habitat types in stream surveys. *North American Journal of Fisheries Management* 15:49-53.
- Roper, B.B., J.L. Kershner, E. Archer, R. Henderson, and N. Bouwes. 2002. An evaluation of physical stream habitat attributes used to monitor streams. *Journal of the American Water Resources Association* 38:1637-1646.
- Rosenberger, A.E. and J.B. Dunham. 2005. Validation of abundance estimates from mark-recapture and removal techniques for rainbow trout captured by electrofishing in small streams. *North American Journal of Fisheries Management* 25:1395-1410.
- Rosenfeld, J.S. and T. Hatfield. 2006. Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* 63:683-698.

- Rubidge, E.M. and E.B. Taylor. 2004. Hybrid zone structure and the potential role of selection in hybridizing populations of native westslope cutthroat trout (*Oncorhynchus clarki lewisi*) and introduced rainbow trout (*O. mykiss*). *Molecular Ecology* 13:3735-3749.
- Rubidge, E.M. and E.B. Taylor. 2005. An analysis of spatial and environmental factors influencing hybridization between native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and introduced rainbow trout (*O. mykiss*) in the upper Kootenay River drainage, British Columbia. *Conservation Genetics* 6:369-384.
- Ruckelshaus, M.H., P. Levin, J.B. Johnson, and P.M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. *Annual Review of Ecology and Systematics* 33:665-706.
- Rueth, H.M., J.S. Baron, and L.A. Joyce. 2002. Natural resource extraction: past, present, and future. Pages 85-112 in J.S. Baron, editor. *Rocky Mountain futures: an ecological perspective*. Island Press, Washington, D.C.
- Running, S.W. 2006. Is global warming causing more, larger wildfires? *Science* 6 July 2006 (10.1126/science.1130370).
- Sabine, E., G. Schreiber, A.R. Bearlin, S.J. Nicol, and C.R. Todd. 2004. Adaptive management: a synthesis of current understanding and effective application. *Ecological Management & Restoration* 5:177-182.
- Safford, H.D. 1995. The recovery planning blues. *Northwest Science* 69:330-335.
- Sanchez, J. and C. Hirsch. 2001. Species viability report for Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus* on the White River National Forest, Colorado. White River National Forest, 900 Grand Avenue, Glenwood Springs, CO. 18 p.
- Sanz, N., M. Cortey, C. Pla, and J.L. García-Marín. 2006. Hatchery introgression blurs ancient hybridization between brown trout (*Salmo trutta*) lineages as indicated by complementary allozymes and mtDNA markers. *Biological Conservation* 130:278-289.
- Sato, T. 2006. Dramatic decline in population abundance of *Salvelinus leucomaenis* after a severe flood and debris flow in a high gradient stream. *Journal of Fish Biology* 69:1849-1854.
- Saunders, W.C. and K.D. Fausch. 2007. Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. *Transactions of the American Fisheries Society* 136:1216-1230.
- Scarnecchia, D.L. and E.P. Bergersen. 1986. Production and habitat of threatened greenback and Colorado River cutthroat trouts in Rocky Mountain headwater streams. *Transactions of the American Fisheries Society* 115: 382-391.
- Schill, D.J., J.S. Griffith, and R.E. Gresswell. 1986. Hooking mortality of cutthroat trout in a catch-and-release segment of the Yellowstone River, Yellowstone National Park. *North American Journal of Fisheries Management* 6:226-232.
- Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704-712.
- Schlosser, I.J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* 301:71-81.
- Schlosser, I.J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. *Oecologia* 113:260-268.
- Schlosser, I.J. and P.L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. *American Fisheries Society Symposium* 17: 392-401.
- Schlosser, I.J. and L.W. Kallemeyn. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology* 81:1371-1382.
- Schmetterling, D.A. 2000. Redd characteristics of fluvial westslope cutthroat trout in four tributaries to the Blackfoot River, Montana. *North American Journal of Fisheries Management* 20:776-783.

- Schmetterling, D.A. 2001. Seasonal movements of fluvial westslope cutthroat trout in the Blackfoot River drainage, Montana. *North American Journal of Fisheries Management* 21:507-520.
- Schmetterling, D.A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport upstream of Milltown Dam, Montana. *North American Journal of Fisheries Management* 23: 721-731.
- Schmetterling, D.A. and S.B. Adams. 2004. Summer movements within the fish community of a small montane stream. *North American Journal of Fisheries Management* 24:1163-1172.
- Schmetterling, D.A. and J.A. McFee. 2006. Migrations by fluvial largescale suckers (*Catostomus macrocheilus*) after transport upstream of Milltown Dam, Montana. *Northwest Science* 80:18-25.
- Schoennagel, T., T.T. Veblen, W.H. Romme, J.S. Sibold, and E.R. Cook. 2005. ENSO and PDO variability affect drought-induced fire occurrence in Rocky Mountain subalpine forests. *Ecological Applications* 15:2000-2014.
- Schooley, R.L. 2006. Spatial heterogeneity and characteristic scales of species-habitat relationships. *BioScience* 56: 533-537.
- Schrank, A.J. and F.J. Rahel. 2004. Movement patterns in inland cutthroat trout (*Oncorhynchus clarki utah*): management and conservation implications. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1528-1537.
- Schrank, A.J. and F.J. Rahel. 2006. Factors influencing summer movement patterns of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*). *Canadian Journal of Fisheries and Aquatic Sciences* 63:660-669.
- Schrank, A.J., F.J. Rahel, and H.C. Johnstone. 2003. Evaluating laboratory-derived thermal criteria in the field: an example involving Bonneville cutthroat trout. *Transactions of the American Fisheries Society* 132:100-109.
- Schwartz, M.K., G. Luikart, and R.S. Waples. 2007. Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology and Evolution* 22:25-33.
- Scudder, G.G.E. 1989. The adaptive significance of marginal populations: a general perspective. Pages 180-185 in C.D. Levings, L.B. Holtby, and M.A. Henderson, editors. *Proceedings on the national workshop on effects of habitat alteration on salmonid stocks*. Canadian Special Publication of Fisheries and Aquatic Sciences 105.
- Seager, R., and 12 others. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316:1181-1184.
- Sealing, C., L. Ulmer, C. Cesar, J. Thompson, D. Gerhardt, and T. Fratt. 1992. Conservation plan for Colorado River cutthroat trout in northwest Colorado. Colorado Division of Wildlife, Grand Junction, CO. 20 p.
- Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. MacMillan Publishing Company, NY.
- Seegrist, D.W. and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society* 101:478-482.
- Sestrich, C.M. 2005. Changes in native and nonnative fish assemblages and habitat following wildfire in the Bitterroot River basin, Montana. Master's thesis, Montana State University, Bozeman, MT.
- Shackell, N.L., K.T. Frank, and D.W. Brickman. 2005. Range contraction may not always predict core areas: an example from marine fish. *Ecological Applications* 15:1440-1449.
- Shepard, B.B. 2004. Factors that may be influencing nonnative brook trout invasion and their displacement of native westslope cutthroat trout in three adjacent southwestern Montana streams. *North American Journal of Fisheries Management* 24:1088-1100.
- Shepard, B. 2007. Fisheries Biologist, Montana Fish, Wildlife, and Parks, Bozeman, MT. Personal communication.
- Shepard, B.B. and L. Nelson. 2004. Conservation of westslope cutthroat trout by removal of brook trout using electrofishing: 2001-2003. Report to Montana Fish, Wildlife and Parks Future Fisheries Improvement Program.

- Shepard, B.B., B.E. May, and W. Urie. 2005. Status and conservation of westslope cutthroat trout within the western United States. *North American Journal of Fisheries Management* 25:1426-1440.
- Shepard, B.B., K.L. Pratt, and P.J. Graham. 1984. Life histories of westslope cutthroat and bull trout in the upper Flathead River basin, Montana. Environmental Protection Agency, Region VIII, Water Division, Denver, Colorado. Contract R008224-01-5.
- Shepard, B.B., R. Spoon, and L. Nelson. 2002. A native westslope cutthroat trout population responds positively after brook trout removal and habitat restoration. *Intermountain Journal of Sciences* 8:191-211.
- Shepard, B.B., B. Sanborn, L. Ulmer, and D.C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the upper Missouri River basin, Montana. *North American Journal of Fisheries Management* 17:1158-1172.
- Shiozawa, D. and P. Evans. 2007. Professor, Department of Biology, and Assistant Professor, Department of Microbiology and Molecular Biology, Brigham Young University, Provo, UT. Personal communication.
- Sloat, M.R., R.G. White, and B.B. Shepard. 2002. Status of westslope cutthroat trout in the Madison River basin: influence of dispersal barriers and stream temperature. *Intermountain Journal of Sciences* 8:153-177.
- Smith, G.R., T.E. Dowling, K.W. Gobalet, T. Lugaski, D.K. Shiozawa, and R.P. Evans. 2002. Biogeography and timing of evolutionary events among Great Basin fishes. Pages 175-234 *in* R. Hershler, D.B. Madsen, and D.R. Curry, editors. Great Basin aquatic systems history. Smithsonian Contributions to the Earth Sciences 33.
- Snyder, C.D., J.A. Young, D.P. Lemarié, and D.R. Smith. 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59:262-275.
- Snyder, D.E. 2003. Electrofishing and its harmful effects on fish. U.S. Geological Survey, Denver, Colorado. Information and Technology Report USGS/BRD/ITR-2003-0002.
- Snyder, G.R. and H.A. Tanner. 1960. Cutthroat trout reproduction in the inlets to Trappers Lake. Colorado Department of Game and Fish, Denver. Technical Bulletin 7.
- Soulé, M.E. 1987. Introduction. Pages 1-10 *in* M.E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, UK.
- Soulé, M.E. and M.A. Sanjayan. 1998. Conservation targets: do they help? *Science* 279:2060-2061.
- Speas, C., M. Fowden, M. Gorges, T. Rinkes, G. Eaglin, and B. Wengert. 1994. Conservation plan for Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) for the Little Snake River drainage in southeastern Wyoming. Medicine Bow National Forest, Laramie, WY. 49 p.
- Spens, J., A. Alanärä, and L.-O. Eriksson. 2007. Nonnative brook trout (*Salvelinus fontinalis*) and the demise of native brown trout (*Salmo trutta*) in northern boreal lakes: stealthy, long-term patterns? *Canadian Journal of Fisheries and Aquatic Sciences* 64:654-664.
- Stankey, G.H., R.N. Clark, and B.T. Bormann. 2005. Adaptive management of natural resources: theory, concepts, and management institutions. USDA Forest Service General Technical Report PNW-GTR-654.
- Staples, D.F., M.L. Taper, and B.B. Shepard. 2005. Risk-based viable population monitoring. *Conservation Biology* 19:1908-1916.
- Stapp, P. and G.D. Hayward. 2002. Effects of an introduced piscivore on native trout: insights from a demographic model. *Biological Invasions* 4:299-316.
- Stearley, R.F. 1992. Historical ecology of Salmoninae, with special reference to *Oncorhynchus*. Pages 622-658 *in* R.L. Mayden, editor. Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford, CA.
- Stearley, R.F. and G.R. Smith. 1993. Phylogeny of the Pacific trouts and salmon (*Oncorhynchus*) and genera of the family Salmonidae. *Transactions of the American Fisheries Society* 122:1-33.
- Stearns, S. 1992. The evolution of life histories. Oxford University Press, Oxford.

- Stelfox, J.D., D.M. Baayens, A.J. Paul, and G.E. Shumaker. 2001. Quirk Creek brook trout suppression project. Pages 37-46 in M.K. Brewin, A.J. Paul, and M. Monita. Bull Trout II Conference Proceedings.
- Stevens, D.L., Jr. and A.R. Olsen. 1999. Spatially restricted surveys over time for aquatic resources. *Journal of Agricultural, Biological, and Environmental Statistics* 4:415-428.
- Stewart, I.T., D.R. Cayan, and M.D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. *Journal of Climate* 18:1136-1155.
- Stockwell, C.A. and P.L. Leberg. 2002. Ecological genetics and the translocation of native fishes: merging experimental approaches. *Western North American Naturalist* 62:32-38.
- Stockwell, C.A., A.P. Hendry, and M.T. Kinnison. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* 18:94-101.
- Stolnack, S.A., M.D. Bryant, and R.C. Wissmar. 2005. A review of protocols for monitoring streams and juvenile fish in forested regions of the Pacific Northwest. USDA Forest Service General Technical Report PNW-GTR-625.
- Strange, C.D., M.W. Aprahamian, and A.J. Winstone. 1989. Assessment of a semi-quantitative electric fishing sampling technique for juvenile Atlantic salmon, *Salmo salar* L., and trout, *Salmo trutta* L., in small streams. *Aquaculture and Fisheries Management* 20:485-492.
- Strayer, D.L. 1999. Statistical power of presence-absence data to detect population declines. *Conservation Biology* 13:1034-1038.
- Swanberg, T.R. 1997. Movements of bull trout (*Salvelinus confluentus*) in the Clark Fork River system after transport upstream of Milltown Dam. *Northwest Science* 71:313-317.
- Sweka, J.A., C.M. Legault, K.F. Beland, J. Trial, and M.J. Milliard. 2006. Evaluation of removal sampling for basinwide assessment of Atlantic salmon. *North American Journal of Fisheries Management* 26:995-1002.
- Tallmon, D.A., G. Luikart, and R.S. Waples. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology and Evolution* 19:489-496.
- Taylor, E.B., M.D. Stamford, and J.S. Baxter. 2003. Population subdivision in westslope cutthroat trout (*Oncorhynchus clarki lewisi*) at the northern periphery of its range: evolutionary inferences and conservation. *Molecular Ecology* 12:2609-2622.
- Temple, G.M. and T.N. Pearsons. 2006. Evaluation of the recovery period in mark-recapture population estimates of rainbow trout in small streams. *North American Journal of Fisheries Management* 26:941-948.
- Theobald, D.M. and N.T. Hobbs. 2002. Collaborative development of a conservation planning system: a case study of Summit County, Colorado. Pages 255-268 in J.S. Baron, editor. *Rocky Mountain futures: an ecological perspective*. Island Press, Washington, D.C.
- Thomas, V.G. 1985. Experimentally determined impacts of a small, suction gold dredge on a Montana stream. *North American Journal of Fisheries Management* 5:480-488.
- Thompson, D.M. 2006. Did the pre-1980 use of in-stream structures improve streams? A reanalysis of historical data. *Ecological Applications* 16:784-796.
- Thompson, K.G., R.B. Nehring, D.C. Bowden, and T. Wygant. 1999. Field exposure of seven species or subspecies of salmonids to *Myxobolus cerebralis* in the Colorado River, Middle Park, Colorado. *Journal of Aquatic Animal Health* 11:312-329.
- Thompson, P.D. and F.J. Rahel. 1996. Evaluation of depletion-removal electrofishing of brook trout in small Rocky Mountain streams. *North American Journal of Fisheries Management* 16:332-339.
- Thompson, P.D. and F.J. Rahel. 1998. Evaluation of artificial barriers on small Rocky Mountain streams for preventing the upstream movement of brook trout. *North American Journal of Fisheries Management* 18:206-210.
- Thompson, W.L. 2003. Hankin and Reeves' approach to estimating fish abundance in small streams: limitations and alternatives. *Transactions of the American Fisheries Society*. 132:69-75.

- Thompson, W.L., G.C. White, and C. Gowan. 1998. Monitoring vertebrate populations. Academic Press, San Diego, CA.
- Thurow, R.F. and J.G. King. 1994. Attributes of Yellowstone cutthroat trout redds in a tributary of the Snake River, Idaho. *Transactions of the American Fisheries Society* 123:37-50.
- Thurow, R.F. and D.J. Schill. 1996. Comparison of day snorkeling, night snorkeling, and electrofishing to estimate bull trout abundance and size structure in a second-order Idaho stream. *North American Journal of Fisheries Management* 16:314-323.
- Thurow, R.F., D.C. Lee, and B.E. Rieman. 1997. Distribution and status of seven native salmonids in the interior Columbia River basin and portions of the Klamath River and Great Basins. *North American Journal of Fisheries Management* 17:1094-1110.
- Thurow, R.F., J.T. Peterson, and J.W. Guzevich. 2006. Utility and validation of day and night snorkel counts for estimating bull trout abundance in first- to third-order streams. *North American Journal of Fisheries Management* 26:217-232.
- Torgersen, C.E., R.E. Gresswell, and D.S. Bateman. 2004. Pattern detection in stream networks: quantifying spatial variability in fish distribution. Pages 405-420 *in* T. Nishida, P.J. Kailola, and C.E. Hollingworth, editors. *GIS/spatial analyses in fishery and aquatic sciences (volume 2)*. Fishery-Aquatic GIS Research Group, Saitama, Japan.
- Travis, W.R., D.M. Theobald, and D.B. Fagre. 2002. Transforming the Rockies: human forces, settlement patterns, and ecosystem effects. Pages 1-24 *in* J.S. Baron, editor. *Rocky Mountain futures: an ecological perspective*. Island Press, Washington, D.C.
- Trombulak, S.C. and C. Frissell. 2000. A review of the ecological effects of roads on terrestrial and aquatic ecosystems. *Conservation Biology* 14:18-30.
- Urquhart, N.S., S.G. Paulsen, and D.P. Larsen. 1998. Monitoring for policy-relevant regional trends over time. *Ecological Applications* 8:246-257.
- U.S. Department of Energy. 2006. International energy outlook 2006. Energy Information Administration, Office of Integrated Analysis and Forecasting. DOE/EIA-0484(2006).
- U.S. Fish and Wildlife Service. 1998. Greenback cutthroat trout recovery plan. Denver, CO.
- U.S. Fish and Wildlife Service. 2003. Gila trout recovery plan (third revision). Albuquerque, NM.
- U.S. Fish and Wildlife Service. 2004. 90-day finding on a petition to list the Colorado River cutthroat trout. *Federal Register* 69:21151-21158.
- U.S. Fish and Wildlife Service. 2007. 12-month finding for a petition to list the Colorado River cutthroat trout as threatened or endangered. *Federal Register* 72:32589-32605.
- Utah Division of Wildlife Resources. 2000. Cutthroat trout management: a position paper. Genetic considerations associated with cutthroat trout management. Utah Division of Wildlife Resources, Salt Lake City. Publication 00-26. Available at: <http://www.wildlife.utah.gov/pdf/cuttpos.pdf>. Accessed 17 April 2006.
- Utah Division of Wildlife Resources. 2005. Utah sensitive species list. Available at: <http://dwrcdc.nr.utah.gov/ucdc/ViewReports/SSL020805.pdf>. Accessed 29 November 2005.
- Utter, F.M. and F.W. Allendorf. 1994. Phylogenetic relationships among species of *Oncorhynchus*: a consensus view. *Conservation Biology* 8:864-867.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Veblen, T.T., K.S. Hadley, E.M. Nel, T. Kitzberger, M. Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. *Journal of Ecology* 82:125-135.

- Vincent, E.R. 1983. Fish population estimation techniques in Montana. Proceedings of the Annual Conference of the Western Association of Fish and Wildlife Agencies 63:109-115.
- Vincent, E.R. 1996. Whirling disease and wild trout: the Montana experience. Fisheries 21(6):32-33.
- Vinyard, G.L. and A. Winzeler. 2000. Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) spawning and downstream migration of juveniles into Summit Lake, Nevada. Western North American Naturalist 60: 333-341.
- Vokoun, J.C., C.F. Rabeni, and J.S. Stanovick. 2001. Sample-size requirements for evaluating population size structure. North American Journal of Fisheries Management 21:660-665.
- Vore, D.W. 1993. Size, abundance, and seasonal habitat utilization of an unfished trout population and their response to catch and release fishing. Master's thesis, Montana State University, Bozeman, MT.
- Walters, C.J. 1986. Adaptive management of renewable resources. Macmillan, NY.
- Wang, L. and R.J. White. 1994. Competition between wild brown trout and hatchery greenback cutthroat trout of largely wild parentage. North American Journal of Fisheries Management 14:488-499.
- Waples, R.S. 2002. Definition and estimation of effective population size in the conservation of endangered species. Pages 147-168 in S.R. Beissinger and D.R. McCullough, editors. Population viability analysis. University of Chicago Press, Chicago, IL.
- Waples, R.S. and 15 others. 2001. Characterizing diversity in salmon from the Pacific Northwest. Journal of Fish Biology 59 (Supplement A):1-41.
- Ward, B.R. 2000. Declivity in steelhead (*Oncorhynchus mykiss*) recruitment at the Keogh River over the past decade. Canadian Journal of Fisheries and Aquatic Sciences 57:298-306.
- Wares, J.P., D. Alo, and T.F. Turner. 2004. A genetic perspective on management and recovery of federally endangered trout (*Oncorhynchus gilae*) in the American Southwest. Canadian Journal of Fisheries and Aquatic Sciences 61: 1890-1899.
- Warren, C.E., J.H. Wales, G.E. Davis, and P. Douderoff. 1964. Trout production in an experimental stream enriched with sucrose. Journal of Wildlife Management 28:617-660.
- Warren, D.R. and C.E. Kraft. 2003. Brook trout (*Salvelinus fontinalis*) response to wood removal from high-gradient streams of the Adirondack Mountains (N.Y., U.S.A.). Canadian Journal of Fisheries and Aquatic Sciences 60: 379-389.
- Watts, A.B. 2001. Isostasy and flexure of the lithosphere. Cambridge University Press, Cambridge, UK.
- Wedekind, C., G. Rudolfson, A. Jacob, D. Urbach, and R. Müller. 2007. The genetic consequences of hatchery-induced sperm competition in a salmonid. Biological Conservation 137:180-188.
- Weigel, D.E., J.T. Peterson, and P. Spruell. 2002. A model using phenotypic characteristics to detect introgressive hybridization in wild westslope cutthroat trout and rainbow trout. Transactions of the American Fisheries Society 131:389-403.
- Weigel, D.E., J.T. Peterson, and P. Spruell. 2003. Introgressive hybridization between native cutthroat trout and introduced rainbow trout. Ecological Applications 13:38-50.
- Weigel, D.E. and P.W. Sorensen. 2001. The influence of habitat characteristics on the longitudinal distribution of brook, brown, and rainbow trout in a small Midwestern stream. Journal of Freshwater Ecology 16:599-613.
- Wenburg, J.K. and P. Bentzen. 2001. Genetic and behavioral evidence for restricted gene flow among coastal cutthroat trout populations. Transactions of the American Fisheries Society 130:1049-1069.
- Wengert, B. 2006. Fisheries Biologist, Wyoming Game and Fish Department, Green River, WY. Personal communication.
- Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increases western U.S. forest wildfire activity. Science 6 July 2006 (10.1126/science.1128834).

- White, G.C., D.R. Anderson, K.P. Burnham, and D.L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, NM.
- Whitlock, C., M.A. Reaser, and C.H. Key. 2002. Paleoenvironmental history of the Rocky Mountain region during the past 20,000 years. Pages 41-57 in J.S. Baron, editor. Rocky Mountain futures: an ecological perspective. Island Press, Washington, D.C.
- Wildman, T.L. and R.M. Neumann. 2003. Comparison of snorkeling and electrofishing for estimating abundance and size structure of brook trout and brown trout in two southern New England streams. *Fisheries Research* 60: 131-139.
- Wiley, M.J., S.L. Kohler, and P.W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. *Freshwater Biology* 37:133-148.
- Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and management of animal populations. Academic Press, NY.
- Williams, J.E. and eight others. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries* 14(6):2-20.
- Williams, J.E., D.W. Sada, C.D. Williams, and other members of the Western Division Endangered Species Committee. 1988. American Fisheries Society guidelines for introductions of threatened and endangered fishes. *Fisheries* 13(5):5-11.
- Williams, L.R., M.L. Warren, Jr., S.B. Adams, J.L. Arvai, and C.M. Taylor. 2004. Basin visual estimation technique (BVET) and representative reach approaches to wadeable stream surveys: methodological limitations and future directions. *Fisheries* 29(8):12-22.
- Willson, M.F. 1997. Variation in salmonid life histories: patterns and perspectives. USDA Forest Service Research Paper PNW-RP-498.
- Wiltzius, W.J. 1985. Fish culture and stocking in Colorado, 1872-1978. Division Report 12. Colorado Division of Wildlife, Denver, CO.
- Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). *Canadian Journal of Fisheries and Aquatic Sciences* 42:1668-1672.
- Wilzbach, M.A. and J.D. Hall. 1985. Prey availability and foraging behavior of cutthroat trout in an open and forested section of stream. *Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 22: 2516-2522.
- Wilzbach, M.A., K.W. Cummins, and J.D. Hall. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. *Ecology* 67:898-911.
- Wilzbach, M.A., B.C. Harvey, J.L. White, and R.J. Nakamoto. 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 62:58-67.
- Winters, D.S. and six others. 2004. Anthropogenic influences used in conducting multiple scale aquatic, riparian, and wetland ecological assessments for the USDA Forest Service – Rocky Mountain Region. USDA Forest Service, Rocky Mountain Region, Denver, CO.
- Wipfli, M.S., J.P. Hudson, and J.P. Caouette. 2004. Restoring productivity of salmon-based food webs: contrasting effects of salmon carcass and salmon analog additions on stream-resident salmonids. *Transactions of the American Fisheries Society* 133:1440-1454.
- Withler, F.C. 1982. Transplanting Pacific salmon. Canadian Technical Report of Fisheries and Aquatic Sciences 1079.
- Wofford, J.E.B., R.E. Gresswell, and M.A. Banks. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. *Ecological Applications* 15:628-637.

- Wohl, E.E. 2001. Virtual rivers: lessons from the mountain rivers of the Colorado front range. Yale University Press, New Haven, CT.
- Wohl, E.E. 2004. Disconnected rivers: linking rivers to landscapes. Yale University Press, New Haven, CT.
- Wroten, W.H. 1956. The railroad tie industry in the central Rocky Mountain region: 1867-1900. Doctoral dissertation, University of Colorado, Boulder, CO.
- Wyatt, R.J. 2002. Estimating riverine fish population size from single- and multiple-pass removal sampling using a hierarchical model. *Canadian Journal of Fisheries and Aquatic Sciences* 59:695-706.
- Wyoming Game and Fish Commission. 2001. Native species status of fish and amphibian species native to Wyoming. Wyoming Game and Fish Department, Cheyenne, WY.
- Wyoming Game and Fish Department. 2007. Wyoming Game and Fish Department management activities for Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*). Fish Division, Wyoming Game and Fish Department, Cheyenne, WY.
- Yamamoto, S., K. Morita, and A. Goto. 1999. Geographic variations in life-history characteristics of white-spotted charr (*Salvelinus leucomaenis*). *Canadian Journal of Zoology* 77:871-878.
- Yoccoz, N.G., J.D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* 16:446-453.
- Young, M.K. 1995a. Colorado River cutthroat trout. Pages 16-23 in M.K. Young, technical editor. Conservation assessment for inland cutthroat trout. USDA Forest Service General Technical Report RM-GTR-256.
- Young, M.K. 1996. Summer movements and habitat use by Colorado River cutthroat trout in small, montane streams. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1403-1408.
- Young, M.K. 1998. Absence of autumnal changes in habitat use and location of adult Colorado River cutthroat trout. *Transactions of the American Fisheries Society* 127:147-151.
- Young, M.K. 1999. Summer diel activity and movement of adult brown trout in high-elevation streams in Wyoming, U.S.A. *Journal of Fish Biology* 54:181-189.
- Young, M.K. and P.M. Guenther-Gloss. 2004. Population characteristics of greenback cutthroat trout in streams: their relation to model predictions and recovery criteria. *North American Journal of Fisheries Management* 24: 184-197.
- Young, M.K. and A.L. Harig. 2001. A critique of the recovery of greenback cutthroat trout. *Conservation Biology* 15: 1575-1584.
- Young, M.K. and D.A. Schmetterling. 2004. Electrofishing and salmonid movement: reciprocal effects in two small montane streams. *Journal of Fish Biology* 64:750-761.
- Young, M.K., R.E. Gresswell, and C.H. Luce, editors. 2003. The effects of wildland fire on aquatic ecosystems in the western USA. *Forest Ecology and Management* 178.
- Young, M.K., P.M. Guenther-Gloss, and A.D. Ficke. 2005. Predicting cutthroat trout (*Oncorhynchus clarkii*) abundance in high-elevation streams: revisiting a model of translocation success. *Canadian Journal of Fisheries and Aquatic Sciences* 62:2399-2408.
- Young, M.K., D. Haire, and M.A. Bozek. 1994. The impact and extent of railroad tie drives in streams of southeastern Wyoming. *Western Journal of Applied Forestry* 9:125-130.
- Young, M.K., W.A. Hubert, and T.A. Wesche. 1989. Substrate alteration by spawning brook trout in a southeastern Wyoming stream. *Transactions of the American Fisheries Society* 118:379-385.
- Young, M.K., W.A. Hubert, and T. A. Wesche. 1991. A comparison of different measures of substrate composition and their relation to survival to emergence of embryonic salmonids. *North American Journal of Fisheries Management* 11:339-346.

- Young, M.K., B.K. Micek, and M. Rathbun. 2003. Probable pheromonal attraction of sexually mature brook trout to mature male conspecifics. *North American Journal of Fisheries Management* 23:276-282.
- Young, M.K., R.B. Rader, and T.A. Belish. 1997a. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River cutthroat trout. *Transactions of the American Fisheries Society* 126:428-437.
- Young, M.K., A.L. Harig, B. Rosenlund, and C. Kennedy. 2002. Recovery history of greenback cutthroat trout: population characteristics, hatchery involvement, and bibliography. Version 1.0. Rocky Mountain Research Station RMRS-GTR-88WWW. Available at http://www.fs.fed.us/rm/pubs/rmrs_gtr88.
- Young, M.K., E.A. Mace, E.T. Ziegler, and E.K. Sutherland. 2006. Characterizing and contrasting instream and riparian coarse wood in western Montana streams. *Forest Ecology and Management* 226:26-40.
- Young, M.K., K.A. Meyer, D.J. Isaak, and R.A. Wilkison. 1998. Habitat selection and movement by individual cutthroat trout in the absence of competitors. *Journal of Freshwater Ecology* 13:371-381.
- Young, M.K., R.N. Schmal, T.W. Kohley, and V.G. Leonard. 1996. Conservation status of Colorado River cutthroat trout. USDA Forest Service General Technical Report RM-GTR-282.
- Young, M.K., R.A. Wilkison, J.M. Phelps, and J.S. Griffith. 1997b. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. *Great Basin Naturalist* 57:238-244.
- Young, S.F., J.G. McLellan, and J.B. Shaklee. 2004. Genetic integrity and microgeographic population structure of westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in the Pend Oreille Basin in Washington. *Environmental Biology of Fishes* 69:127-142.
- Youngson, A.F., W.C. Jordan, E. Verspoor, P. McGinnity, T. Cross, and A. Ferguson. 2003. Management of salmonid fisheries in the British Isles: towards a practical approach based on population genetics. *Fisheries Research* 62: 193-209.
- Zalewski, M. 1985. The estimate of fish density and biomass in rivers on the basis of relationships between specimen size and efficiency of electrofishing. *Fisheries Research* 3:147-155.
- Zalewski, M. and I.G. Cowx. 1990. Factors affecting the efficiency of electric fishing. Pages 89-111 in I.G. Cowx and P. Lamarque, editors. *Fishing with electricity: applications in freshwater fisheries management*. Fishing News Books, Oxford.
- Zurstadt, C.F. and K. Stephan. 2004. Seasonal migration of westslope cutthroat trout in the Middle Fork Salmon River drainage, Idaho. *Northwest Science* 78:278-285.
- Zydlewski, G.B. and J.R. Johnson. 2002. Response of bull trout fry to four types of water diversion screens. *North American Journal of Fisheries Management* 22:1276-1282.

The U.S. Department of Agriculture (USDA) prohibits discrimination in all its programs and activities on the basis of race, color, national origin, age, disability, and where applicable, sex, marital status, familial status, parental status, religion, sexual orientation, genetic information, political beliefs, reprisal, or because all or part of an individual's income is derived from any public assistance program. (Not all prohibited bases apply to all programs.) Persons with disabilities who require alternative means for communication of program information (Braille, large print, audiotope, etc.) should contact USDA's TARGET Center at (202) 720-2600 (voice and TDD). To file a complaint of discrimination, write to USDA, Director, Office of Civil Rights, 1400 Independence Avenue, S.W., Washington, DC 20250-9410, or call (800) 795-3272 (voice) or (202) 720-6382 (TDD). USDA is an equal opportunity provider and employer.